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The genus *Euploea* (Lep. Danaidae) in Micronesia, Melanesia,
Polynesia and Australia. A zoo-geographical study.

By

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(With Plates 1-9.)

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INTRODUCTION.

This study was commenced some twenty years ago, in an investigation of the curiously white marked association of *Euploea* butterflies on San Cristobal and its small neighbours at the south-east end of the British Solomon Islands: this resulted in a survey of all the Solomons to ascertain the relationships of the *Euploea* fauna. Bougainville having thus come into the picture it became necessary to consider Papua and the Bismarck Archipelago, and then the other archipelagoes (Lousiade, D'Entrecasteaux, and Trobriand). In the other direction Santa Cruz led on to the Banks, Torres, New Hebrides and New Caledonia islands, and Australia soon became involved. Fiji and the chain

* Professor Hale Carpenter died while the paper was in proof and his friends, Professor G. C. Varley and Mr. N. D. Riley very kindly undertook to see the monograph through the Press.

of islands to the east, as far as *Euploea* was found, completed the survey. Finally it was thought worth while to include the few islands of Micronesia in which *Euploea* occurs and thus cover the whole of Micronesia, Melanesia, and Polynesia.

New Guinea has many forms which are not represented in these islands, and they are not considered. Islands west of New Guinea have little relation to those discussed except for the Moluccas which have an important bearing on the origin of some of the Solomons forms.

The number of specimens here recorded, that have been examined in detail, is 9,142, and very many others were seen and discarded for inadequate data.

The following are the sections into which this paper is divided.

- (1) A taxonomic roll of the forms considered, numbering 137. The word "form" is used in its widest sense to indicate an entity sufficiently distinct from others to deserve a name. In this list, only, an attempt is made to distinguish between "species"—"subspecies"—or "form" in its narrowest sense.
- (2) Description of each form according to its spot-pattern. Eighteen new subspecies and forms are described, and old types redescribed. The four systems of spots are described, peculiarities noticed, and the maximal and minimal development for each form, and each sex, is given.
- (3) Distribution of each form with the number of each sex for each island.
- (4) Faunistic. The whole area is divided into sub-areas according to the character of the *Euploea* fauna; for each island of a sub-area details of its *Euploea* fauna, with numbers, are given. By this the significance of absence can be evaluated. From this section and the preceding, the distribution of each form and the fauna of each island can be considered.
- (5) Relationships of each sub-area. The fauna of each sub-area is discussed in relation to others, and an attempt is made to understand its origin. Some reference to recent work on other insects is made, and comparison with results obtained by E. Mayr for birds of the same region.
- (6) A short list of specimens with anomalous distribution.
- (7) The white-bordered associations on Malaita, San Cristobal and its smaller neighbours.
- (8) Acknowledgments.
- (9) Summary.
- (10) Addenda.
- (11) References.

Note. Names of islands are spelt in accordance with the *Geographical Handbook, Pacific Islands*, Vol. 3, Western Pacific, published in 1944 (for official use only) and consulted at the School of Geography, Oxford.

PART 1. TAXONOMIC ROLL AND ENUMERATIONS.

Here follows a list of the "forms" which have been considered; the arrangement with rare diversions is drawn up in accordance with that carried out by the late A. S. Corbet in the British Museum (Nat. Hist.) shortly before his premature

and lamented death in 1948. The precise taxonomic rank of each named entity is an extremely difficult problem, for too little is known of their ecology.

One presumes that if two definite forms occur side by side in the same area without intermediates they should be classed as "species", yet it seems that a form which by isolation has developed into a subspecies may at a later date trespass into the area of another subspecies and the two may be collected at the same time and place. Sometimes, as in the interesting series of *tulliolus* forms kindly sent me by Professor Remington from Yale, these may then interbreed and produce intermediates as true subspecies are supposed to do. In such cases the invader may be presumed to be the one in the minority. There may be, as with *eurianassa* and *treitschkei* (see pp. 102 and 105) several named forms in the same locality, often strikingly different and presenting a parallel with the polymorphic African Nymphaline *Pseudacraea eurytus* L. (*Trans. R. ent. Soc. Lond.* 1949, **100**, 71-133). An excellent example is furnished by No. 19, *cerberus*, Nos. 20, *subpunctata*, and 22, *obscura*, all occurring on New Ireland and with difficulty separable.

Toxopeus (1950) has devised a term "species duplex", in these words—"A species duplex is one which is represented twice in the same district by autonomous subspecies. This may be the result of a double immigration by subspecies that cannot interbreed or which are disinclined to interbreed in nature. In regard to the species complex, *i.e.*, the whole compound of subspecies taken together, they both occupy the position of subspecies, *i.e.*, of local representatives. In many cases the behaviour of the components of a species duplex have changed somewhat in course of time, often a species duplex will consist of an old resident subspecies and a new intruder."

Cases of this sort can be found in the Solomons, *e.g.*, *brenchleyi*, an apparently well established and abundant form of *boisduvalii* and the newly discovered form *albomarginata* which is more like the smaller forms in the Santa Cruz area and has probably been derived from one of them.

Corbet (1943) separated the Indo-Australian *Euploea* into eleven groups of which the following do not enter our region—*martinii* (No. 4), *mulciber* (No. 5) and *gamelia* (No. 6), while No. 11, *midamus*, is only represented by the *leucostictos* complex. Corbet did not employ the term "super-species", and I have in some cases classified the forms somewhat differently. Thus, he uses *leucostictos* to include, as a "complex", not only the diverse forms of *leucostictos* Gmelin, 1790, but also the numerous forms under *nemertes* Hübner, 1806. Since *leucostictos*, *sensu stricto*, does not enter the South Pacific, whereas that area belongs to *nemertes*, I prefer to keep the latter with *usipetes* Hewitson, 1858, separate. Similarly, I prefer three groupings under *tulliolus*, for *tulliolus* F., 1793; for *stephensii* C. & R. Felder, 1865; and for *darchia* W. S. Macleay, 1826, with their numerous forms.

The complete name, bi- or tri-nomial, of each form with author and date is given in the following list, with a serial number. Afterwards, for brevity, only the terminal item of a name will be used with its serial number to enable the reader to refer back to the full name and taxonomic position. The attempt to indicate the taxonomic status of each item is based on consideration of its

appearance, and distribution, especial attention being paid to the apparent degree of geographical isolation.

Group A (*climena*).

F.W. with recurrent vein in cell, no brand.

H.W. without raised pale patch in cell area.

Name	Rank	Synonymy
LEWINII COMPLEX		
(1) <i>brunnescens</i> mihi	Geogr. R. (new)	
(2) <i>lilybaea</i> Fruhstorfer, 1911	Geogr. R.	
(3) <i>montrouzieri</i> C. & R. Felder, 1865	Geogr. R.	(Formerly wrongly known as <i>helcita</i> Boisduval, 1859, <i>vide</i> No. 54)
(4) <i>eschschoeltzii</i> Felder, 1865	Geogr. R.	
(5) <i>lauensis</i> Talbot, 1942	Form	
(6) <i>distincta</i> Butler, 1874	Geogr. R.	
(7) <i>lewinii</i> C. & R. Felder, 1865	Geogr. R.	Synonym <i>mathewi</i> Poulton, 1924
(8) <i>bourkei</i> Poulton, 1924	Geogr. R.	
(9) <i>walkeri</i> Druce, 1890	Form	Synonym <i>matilica</i> Fruhstorfer, 1911
(10) <i>perryi</i> Butler, 1874	Geogr. R.	Synonyms <i>intermedia</i> Moore, 1883 ; <i>indistincta</i> Moore, 1883 ; <i>unicolor</i> H. Druce, 1890
CLIMENA COMPLEX		
(11) <i>doretta</i> Pagenstecher, 1894	Geogr. R.	
(12) <i>macleari</i> Butler, 1887	Geogr. R.	Synonym <i>malindeva</i> Waterhouse, 1914
(13) <i>nobilis</i> Strand, 1914	Species	Synonyms <i>simplicior</i> Strand, 1914 ; <i>zavata</i> Strand, 1914
MODESTA COMPLEX		
(14) <i>lugens</i> Butler, 1876	Geogr. R.	Synonym <i>smithii</i> Moore, 1883
(15) <i>misagenes</i> , Fruhstorfer, 1910	Geogr. R.	
(16) <i>wernerii</i> Fruhstorfer, 1909	Geogr. R.	
(17) <i>jennessi</i> Carpenter, 1941	Species ?	
(18) <i>insulicola</i> Strand, 1914	Geogr. R.	
(19) <i>cerberus</i> Butler, 1882	Species	
(20) <i>subpunctata</i> Fruhstorfer, 1910	? Form	
(21) <i>griseitincta</i> Carpenter, 1942	Geogr. R.	
(22) <i>obscura</i> Pagenstecher, 1894	Species	
(23) <i>eboraci</i> Grose Smith, 1894	Species	
WALLACEI COMPLEX		
(24) <i>melia</i> Fruhstorfer, 1904	Form	
(25) <i>catana</i> Fruhstorfer, 1904	Form	
BATESII COMPLEX		
<i>batesii</i> C. & R. Felder	Species	
(26) <i>auritincta</i> mihi	Geogr. R. (new)	
(27) <i>trobriandensis</i> mihi	Geogr. R. (new)	
(28) <i>nanum</i> mihi	Forma nova	
(29) <i>rotunda</i> van Eecke, 1915	Geogr. R.	
(30) <i>belia</i> Waterhouse & Lyell, 1914	Geogr. R.	

(31) <i>resarta</i> Butler, 1876	Geogr. R. ?	Synonyms <i>funerea</i> Butler, 1878 ; <i>squalida</i> Butler, 1878 ; <i>turbonia</i> Fruhstorfer, 1910 ; <i>murena</i> Fruhstorfer, 1911
(32) <i>kunggana</i> mihi	Geogr. R. (new)	
(33) <i>honesta</i> Butler, 1882	Geogr. R.	Synonyms <i>faisina</i> Ribbe, 1898 ; <i>bigamica</i> Strand, 1914
(34) <i>woodfordi</i> , G. & S. 1888	Geogr. R.	
(35) <i>leucacron</i> mihi	Geogr. R. (new)	
ALCATHOE COMPLEX		
<i>alcathoe</i> Godart	Species	
(36) <i>coffea</i> Fruhstorfer, 1910	Form	
(37) <i>diadema</i> Moore, 1883	Form	
(38) <i>macgregori</i> Kirby, 1889	Form	
(39) <i>samaraina</i> mihi	Geogr. R. (new)	
(40) <i>monilifera</i> Moore, 1883	Geogr. R.	Synonym <i>misenus</i> Miskin, 1890
(41) <i>eichhorni</i> Staudinger, 1884	Species	Synonym <i>boreas</i> Miskin, 1889

Group B (*core*).

F.W. with recurrent vein in cell and single brand.

H.W. without raised patch in cell area.

Name	Rank	Synonymy
(42) <i>lacon</i> Grose Smith, 1894	Species	Synonym <i>malaguna</i> Ribbe, 1898
CORE COMPLEX		
(43) <i>corinna</i> Macleay, 1827	Species	Synonyms <i>angasii</i> C. & R. Felder, 1865 ; <i>euclus</i> Miskin, 1890 ; <i>coerti</i> Kalis, 1933
(44) <i>rennelliensis</i> mihi	Species (new)	
(45) <i>umboina</i> mihi	Species ? (new)	
(46) <i>subnobilis</i> Strand, 1914	Species	
(47) <i>illudens</i> Butler, 1882	Species	Synonyms <i>decipiens</i> Butler, 1882 ; <i>lygdamis</i> Fruhstorfer, 1910
(48) <i>mathiasana</i> Carpenter, 1942	Geogr. R.	
ALGEA COMPLEX		
<i>algea</i> Godart	Species	
(49) <i>amycus</i> Miskin, 1890	Geogr. R.	
(50) <i>reginae</i> mihi	Geogr. R. (new)	
(51) <i>irene</i> Fruhstorfer, 1910	Species	
(52) <i>eleutho</i> Godart, 1823	Species	
(53) <i>abjecta</i> Butler, 1866	Species	
(54) <i>helcita</i> Boisduval, 1859	Species	Synonym <i>whitmei</i> Butler, 1877
(55) <i>aglaina</i> Fruhstorfer, 1910	Geogr. R.	Synonym <i>maréensis</i> Poulton, 1927
(56) <i>schmeltzi</i> H-S., 1869	Species	
<i>nechos</i> Mathew	Species	
(57) <i>nechos</i> Mathew, 1887	Geogr. R.	
(58) <i>prusias</i> G. & S., 1888	Geogr. R.	
(59) <i>pronax</i> G. & S., 1888	Geogr. R.	

	<i>boisduvalii</i> Lucas	Species	
(60)	<i>fraudulenta</i> Butler, 1882	Species	Synonym <i>bigamica</i> (♀) Strand, 1914
(61)	<i>pyrgion</i> G. & S., 1888	Geogr. R.	
(62)	<i>brenchleyi</i> Butler, 1870	Geogr. R. ? or Species	
(63)	<i>albomarginata</i> mihi	Geogr. R. or ? Form (new)	
(64)	<i>era</i> de Nicéville, 1902	Geogr. R.	
(65)	<i>lapeyrousei</i> Boisduval, 1832	Geogr. R.	
(66)	<i>matemae</i> mihi	Geogr. R. (new)	
(67)	<i>torvina</i> Butler, 1875	Geogr. R.	
(68)	<i>bakeri</i> Poulton, 1927	Geogr. R.	
(69)	<i>rileyi</i> Poulton, 1923	Geogr. R.	
(70)	<i>herrichii</i> C. & R. Felder, 1865	Form	Synonym <i>proserpina</i> Butler 1866
(71)	<i>boisduvalii</i> Lucas, 1853	Form	
(72)	<i>mangoensis</i> Butler, 1884	Form	Synonym <i>simmondsi</i> Poulton, 1924
(73)	<i>eurianassa</i> Hewitson, 1858	Species	Synonyms <i>cumaxa</i> Fruhstorfer 1910 ; <i>terentilia</i> Fruhstorfer, 1910

Group C (*sylvester*).

F.W. with recurrent vein in cell ; brand present, termen curved.

H.W. without pale raised patch in cell area.

	Name	Rank	Synonymy
	<i>sylvester</i> F.	Species	
(74)	<i>inconspicua</i> Butler, 1878	Form	Synonyms <i>immaculata</i> Butler, 1878 ; <i>limbata</i> Fruhstorfer, 1910 ; <i>tarnis</i> Fruhstorfer, 1910 ; <i>suada</i> Miskin, 1890 ; <i>crithon</i> Miskin, 1890
(75)	<i>moesta</i> Butler, 1866	Form	
(76)	<i>melander</i> Grose Smith, 1897	Geogr. R.	
(77)	<i>magnipunctata</i> Carpenter, 1942	Form	
(78)	<i>tristis</i> Butler, 1866	Geogr. R.	Synonym <i>scylla</i> Fruhstorfer, 1910.
(79)	<i>pelor</i> Dbldy., Hew. & Wwd., 1847	Form	
(80)	<i>sylvester</i> F., 1793	Form	
(81)	<i>dardanoides</i> Waterhouse, 1914	Form	

Group D (*treitschkei*).

F.W. with recurrent vein in cell : brand present, termen curved.

H.W. with pale raised patch in cell area.

	Name	Rank	Synonymy
	<i>treitschkei</i> Boisduval	Species	
(82)	<i>treitschkei</i> Boisduval, 1832	Form	
(83)	<i>eugenia</i> Fruhstorfer, 1910	Geogr. R.	
(84)	<i>dampierensis</i> mihi	Form (nomen novum)	Synonym <i>intermedia</i> Rothschild, 1915 (name pre-occupied by Moore, 1883)
(85)	<i>ursula</i> Butler, 1883	Form	Synonym <i>biformis</i> Butler, 1882
(86)	<i>gaedei</i> Bryk, 1937	Form	Synonyms <i>olivacea</i> Grose Smith, 1894 (name pre-occupied by Moore, 1883) ; <i>hageni</i> Bryk, 1937

(87) <i>caerulescens</i> Ribbe, 1898	Form	
(88) <i>eulegnica</i> mihi	Geogr. R. (new)	
(89) <i>viridis</i> Butler, 1882	Form	Synonym <i>decia</i> Fruhstorfer, 1910
(90) <i>jessica</i> Butler, 1869	Form	Synonyms <i>lorenzo</i> Butler, 1870 ; <i>erimas</i> G. & S., 1878
(91) <i>aenea</i> Butler, 1882	Geogr. R.	Synonym <i>salomonis</i> Ribbe, 1898
(92) <i>suffusca</i> mihi	Geogr. R. (new)	

Group E (*eleusina*).

F.W. without recurrent vein, dorsum strongly bowed, single circular brand.

H.W. costal nacreous area not extending beyond area 5.

Name	Rank	Synonymy
(93) <i>asyllus</i> G. & S., 1888	Species	Synonym <i>laurentia</i> Fruhstorfer, 1910
(94) <i>gerion</i> G. & S., 1888	Geogr. R.	

Group F (*tulliolus*).

F.W. without recurrent vein, dorsum strongly bowed, no brand.

H.W. with prominent pale yellow raised patch extending into cell but not beyond middle.

Name	Rank	Synonymy
TULLIOLUS COMPLEX		
<i>tulliolus</i> F.	Species	
(95) <i>dudgeonis</i> Grose Smith, 1894	Geogr. R.	Synonym <i>vulcanica</i> Rothschild, 1915
(96) <i>tulliolus</i> F., 1793	Geogr. R.	
(97) <i>goodenoughi</i> mihi	Geogr. R. (new)	
(98A) <i>forsteri</i> C. & R. Felder, 1865	Form	Synonym <i>seriata</i> H-S., 1869
(98B) <i>incompta</i> H-S., 1869	Form	Synonym <i>protoforsteri</i> Poulton, 1923
(99) <i>adyte</i> Boisduval, 1859	Geogr. R.	
(100) <i>darchia</i> Macleay, 1827	Geogr. R.	
(101) <i>niveata</i> Butler, 1875	Geogr. R.	
PYRES COMPLEX		
(102) <i>pyres</i> G. & S., 1888	Species	
(103) <i>mangolinella</i> Strand, 1914	Geogr. R.	
(104) <i>paucinotata</i> mihi	Geogr. R. (new)	
STEPHENSII COMPLEX		
<i>stephensii</i> C. & R. Felder	Species	
(105) <i>jamesi</i> Butler, 1876	Geogr. R.	Synonym <i>infantilis</i> Butler, 1876
(106) <i>phokion</i> Fruhstorfer, 1904	Geogr. R.	
(107) <i>salpinxoides</i> Fruhstorfer, 1900	Geogr. R.	
(108) <i>bismarckiana</i> Fruhstorfer, 1900	Geogr. R.	
(109) <i>manusi</i> Carpenter, 1942	Geogr. R.	
(110) <i>nivani</i> mihi	Geogr. R. (new)	

Group G (*phaenareta*).

F.W. without recurrent vein, dorsum bowed, no brand.

H.W. with pale yellow raised patch extending to within 1-2 mm. of median vein.
Saccus and aedeagus remarkably short.

Name	Rank	Synonymy
CALLITHOE COMPLEX		
<i>callithoe</i> Boissduval	Species	
(111) <i>callithoe</i> Boissduval, 1832	Form	
(112A) <i>hansemanni</i> Honrath, 1888	Form	
(112B) <i>durrsteini</i> Staudinger, 1890	Form	
(113) <i>admiralia</i> Strand, 1914	Geogr. R.	
(114) <i>eurykleia</i> Fruhstorfer, 1910	Form	
(115) <i>arova</i> Fruhstorfer, 1913	Form	
PHAENARETA COMPLEX		
<i>phaenareta</i> Schaller	Species	
(116) <i>unibrunnea</i> G. & S., 1877	Geogr. R.	
(117) <i>browni</i> G. & S., 1877	Form	
(118) <i>heurippa</i> G. & S., 1888	Geogr. R.	

Group H (*midamus*).

F.W. without recurrent vein, brand present.

H.W. with prominent pale yellow patch extending into cell to within 1-2 mm. of median vein.

Name	Rank	Synonymy
LEUCOSTICTOS COMPLEX		
(119) <i>kadu</i> Eschscholtz, 1821	Species ?	
NEMERTES COMPLEX		
<i>nemertes</i> Hübner	Species	
(120) <i>eustachius</i> Kirby, 1889	Form	Synonym <i>quintia</i> Fruhstorfer, 1910
(121) <i>aviena</i> Fruhstorfer, 1910	Form	
(122) <i>erima</i> Fruhstorfer, 1899	Form	Synonyms <i>gorima</i> Fruhstorfer, 1910 ; <i>atomaria</i> Fruhstorfer, 1910
(123) <i>rhodia</i> Fruhstorfer, 1910	Form	
(124) <i>messia</i> Fruhstorfer, 1910	Aberration ?	
(125) <i>affinita</i> Strand, 1914	Geogr. R.	Synonym <i>nemertoides</i> Rothschild, 1915
(126) <i>perdita</i> Butler, 1882	Geogr. R.	Synonym <i>ulaguna</i> Ribbe, 1898
(127) <i>pulchella</i> Carpenter, 1942	Geogr. R.	
(128) <i>polymela</i> G. & S., 1888	Geogr. R.	
(129) <i>imitata</i> Butler, 1870	Geogr. R.	
(130) <i>rossi</i> mihi	Geogr. R. (new)	
(131) <i>crucis</i> mihi	Geogr. R. (new)	
(132) <i>eustachiella</i> mihi	Geogr. R. (new)	
(133) <i>iphianassa</i> Butler, 1866	Geogr. R.	Synonym <i>consanguinea</i> Butler, 1878
(134) <i>novarum-ebudum</i> Carpenter, 1942	Geogr. R.	Synonym <i>graeffiana</i> auctorum
(135) <i>macleani</i> C. & R. Felder, 1865	Geogr. R.	Synonym <i>graeffiana</i> H.-S., 1869
<i>usipetes</i> Hewitson	Species	
(136) <i>usipetes</i> Hewitson, 1858	Geogr. R.	Synonym <i>hippias</i> Miskin, 1890
(137) <i>rezia</i> Kirby, 1894	Geogr. R.	

PART 2. SPOT CHARACTERS.

Diagnosis of *Euploea* is often fogged by vagueness in the original descriptions, not only of the long past but even of so recent a writer as Fruhstorfer. Inadequate attention has been paid to the number and arrangement of the various series of spots, which are often of diagnostic value. The following tabular statement shows for each form (using "form" in the widest possible sense for an entity except an individual aberration with sufficient characters to have a name) the precise number and situation of the spots on each surface: details are given for the types, and for each sex the maximal and minimal developments of the spot systems are recorded. Reference to a form is conveniently given through its serial number. Very few specimens show all the possible spots in each series, and for an illustration it has been necessary to select *E. leachii malayica* Butler, 1878 (Pl. 1, fig. 7): among Pacific species *E. asyllus* G. & S., 1888 is very well spotted (Pl. 1, fig. 5) but never has a cell-spot.

The spots are apparently the remains of a pattern of streaks, well shown in many Oriental Danainae and seen in the females of *E. mulciber*, Cramer 1777 (Pl. 1, fig. 6) and *E. euctemon* Hewitson, 1866 (Pl. 1, fig. 3) but not in any of the species here considered. Spots reach their maximal development in females, and on the under-surface in both sexes where alone they may be shown: this suggests that they have aposematic value. Very significant is the fact that, as in *E. treitschkei* forms (Pl. 3), the spots may be dyslegnic on the under-surface of the fore-wing but strongly eulegmic on the hind-wing. Since, in complete repose, it is chiefly the under-surface of the hind-wing that proclaims the character of the butterfly, the eulegmic spots with sharp edges have greater value for conspicuousness.

There is sometimes a curious distinction on the underside between spots of the more basal and the more peripheral series: the former may be blue or bluish-white, the latter, on the same wing, creamy or pure white. Most *Euploea* have a few spots at the extreme base of the hind-wing on the underside, close to the body: these have been disregarded. The systems of spots are four, on each wing:

1. *Admarginal*, very close to the edge of the wing.
2. *Submarginal*, between these and the next.
3. *Discal*. On the hind-wing these are arranged neatly around the end of the cell; on the fore-wing they run across the centre of the wing.
4. *Intra-cellular*, or, for brevity, *Cellular*.

The Admarginal spots.(a) *Fore-wing.*

The areas on both wings are numbered from the inner margin forwards. On the fore-wing the full series of spots extends from area 1a to area 8. There is then a pair in each area except 8, as on the underside of the maximal male of No. 9, *walkeri* (cp. Pl. 2, fig. 4): a pair in 7 is rare, and frequently, when the series is not strongly developed, one member of a pair is lacking and the remaining spot is really a half-pair as shown by its position. Certain areas may be weak in admarginals: thus in No. 2, *lilybaea*, admarginals are only seen in 4 as a trace on the underside of the maximally spotted female, and in No. 4, *eschschoitzii*, as a trace on the underside of the maximally spotted male. Area 4 may

completely lack the admarginals as in No. 54, *helcita*. On the other hand it may be the only representative as in No. 116, *unibrunnea*. The whole series is lacking in all *treitschkei* forms (Pl. 3) and many other species; often they are only present in 1b-3 in minimally spotted males, and in No. 130, *rossi* (Pl. 5, fig. 3) the only admarginals are in 1b.

(b) *Hind-wing.*

The full series consists of pairs in 1b-6 with a singleton in 7 which is often elongated into a linear mark. Rarely, as in No. 43, *corinna*, there is a pair in 7 on the underside. Admarginals may be present on the hind-wing when absent from the fore-wing, and even then may only be in the middle areas, as in the smaller forms of *boisduvalii*. On both wings the admarginals may be prolonged inwards to meet the submarginals and even fuse completely with them: this occurs especially at the posterior angle of the wing. The single patch thus resulting may have little indication of its origin from a pair of admarginals but this is sometimes revealed by the H-shape of the combined patch, as shown very clearly in No. 130, *rossi* (Pl. 5, fig. 3), and in many specimens of No. 31, *resarta* (Pl. 5, fig. 5). There does not seem to be on the hind-wing an area which characteristically lacks admarginals, as may be seen on the fore-wing.

The Submarginal spots.

(a) *Fore-wing.*

The submarginals play a major, or the only, part in the pattern in some species, e.g., No. 96, *tulliolus*: this is especially the case at the apex where 5 and 6 are enlarged, the latter being often the largest spot on the wing as in No. 120, *eustachius*, and in No. 39, *samaraina* (Pl. 4, fig. 1), the only spot on the wing except for two minute discals on the underside. Again, the series may be represented by only those towards the apex as in No. 107, *salpinxoides*. The full complement of submarginals on the fore-wing runs from 1b where the spot is usually small but may be paired, as in No. 16, *wernerii* maximal, or No. 98A, *forsteri*, to 11 in the maximal female of No. 70, *herrichii*. After the submarginals have curved round the apex of the fore-wing they are liable to be confused with the similarly curved discals, as there is very little space between them in the contracted costal areas.

Very commonly the most anterior submarginal is that in area 7: 4 is frequently absent or poorly developed as in No. 54, *helcita*. Spot 3 in all forms of the *lewinii* complex, also in No. 14, *lugens*, and No. 15, *misagenes*, is somewhat displaced inwards from the general line. If also elongated it may meet 3 of the discal series as in No. 70, *herrichii*. This has a curious result in some of the forms of *lewinii* (Pl. 2, figs. 2, 3). Thus, No. 6, *distincta* (Pl. 2, fig. 3) shows a large rounded spot in 3, apparently of the discal series, and counted as such in the table to follow. But the underside of the wing shows that the white spot is the displaced submarginal; the true discal lies at its basal end, distinguished by its blue tint.

Some specimens show the small blue discal almost enveloped by the edge of the white submarginal so that the compound spot is hooked, and finally shows no sign of its conjoint origin and is a simple white patch running quite into the base of the area as in No. 10, *walkeri* (Pl. 2, fig. 4).

(b) *Hind-wing.*

A peculiar feature of the submarginals on the hind-wing is that they are usually paired from 1c to 3, or even to 4, while the anterior spots are single: those in 4.5.6 are often the only representatives as in No. 18, *insulicola*, and many specimens of the *treitschkei* group and *nemertes* complex: 1a is present in *lugens* beneath. Reference to the primitive, streaked, pattern, as shown on Pl. 1, figs. 2, 3, 4, will be of interest.

Elongation of submarginals marks *walkeri*; they may meet the admarginals and fuse with them, especially in the anal region. Large patches are thus formed in No. 73, *eurianassa*, in which the conjoint spots make a single well-defined band parallel with the margin. *E. treitschkei* is remarkable for the position of the submarginals of the hind-wing which are so near to the cell that they intermingle with the middle discals or unite with them (Pl. 3). Thus, if the submarginals are lacking from the inner part of the wing there appears to be a single uniform series of which 2 and 3 belong to discals and 4.5.6. to submarginals. Area 1a, which does not contain a spot may have an elongated streak as in the maximal *eichhorni*, No. 41.

The Discal spots.(a) *Fore-wing.*

Upper side.—The discals are very often absent but in some species, *e.g.*, *treitschkei*, they may be the only spots on the wing: 10 and 11 frequently are the only representatives as in forms of the *lewinii* and *tulliolus* complexes: in many specimens of the forms of *nemertes* 10 alone is present. In exceptional cases discal 12 is present, as in the type of No. 50, *reginae*.

The costal marking usually made by 10 and 11 is formed by 9 and 10 in No. 102, *pyres*, and No. 118, *heurippa*; there is often a gap between 6 and 9 as in No. 43, *corinna*. Spot 5 may be only exceptionally present in a species, as in No. 19, *cerberus*: 7 is very rare but is seen on the underside in the maximal male of No. 68, *bakeri*. If any discals at all are shown, other than those on the costa, they are usually 3 and 4 as in the maximal female of No. 34, *woodfordi* (Pl. 7, fig. 5).

Under side.—The most complete series of discals is best seen on the underside. There are markings used by Corbet (1943) for identification of species in 1a and 1b which are not included here in discal spots. But occasionally a true spot may be shown in 1b, as in No. 60, *fraudulenta*, and No. 61, *pyrgion* (Pl. 7, figs. 3, 7): the complete series runs from 1b to 12. The middle discals are often bifid distally, indicating paired origin, *e.g.*, many specimens of No. 60, *fraudulenta* (Pl. 2, fig. 5): in 2 the discal may be broadly joined to submarginal 2 to make a bar as in *fraudulenta* and in other forms of *boisduvalii*. The fusing of 3 with the inwardly displaced submarginal 3 has been discussed.

The costal members of the series may be only present on the underside, as in some specimens of No. 69, *rileyi*, and (as on the upper side) 10 may be the only representative of the discal series as in forms of *nemertes* or No. 109, *manusi*. The underside of a maximal female of No. 43, *corinna*, has a minute streak in D 12.

(b) *Hind-wing.*

The series may be complete from 1a to 8 as in the maximal female of No. 103, *mangolinella*, but the marking in 1a when present is a streak, as also in 1b in

No. 33, *honesta* (Pl. 6, fig. 5), maximal female. The series often increases in size anteriorly, and the two extremes in the usual set of 1c-7 may be linear: when the full number is incomplete it is those at the ends which drop out. The discal series is very commonly absent from the upper side on the hind-wing when well represented below, as in forms of *lewini*.

The Intra-cellular spot.

The spot in the cell of the fore-wing, near its apex, is much more frequently present below than above, as in members of the *sylvester* group, and is less frequent than on the hind-wing. Certain groups, e.g., *nemertes* and *tulliolus* never have a cell-spot: its complete absence from No. 93, *asyllus* (Pl. 1, fig. 5), is surprising.

An unusual feature, seen in No. 33, *honesta* (Pl. 6, fig. 1), is a cell-spot on the upper side of the fore-wing but not on the underside, and not on the upper side of the hind-wing. The original paired condition is often shown by an accessory as in No. 113, *admiralia*, female type: the accessory may be so large that the cell-spot is spoken of as double as in No. 102, *pyres*, or two equal portions lying close together cause the spot to appear split as in No. 70, *herrichii*, maximal male.

The following tables show at a glance the spots for each named form, but some explanation of contractions is necessary. The sign “+” merely means present; “small” or “min.” (minute) implies a defined spot, but “tr.” (trace) means only a few scales, or if more, an ill defined representation. For the admarginals, “irregular” means that there are some here and there, not in full degree, often differing on the two sides. No entry means no spot. The entries under “Max.” or “Min.” refer to the maximal or minimal number for each series, but these are not necessarily all on one specimen.

A series is normally indicated thus, “1c-7”. A break is indicated by “:” and a spot in a series about which something especial is said has a “,” on each side of it. Thus, “1c-2, small 3, 4 : 6-7” indicates that 3 is smaller than would be expected in that series, and 5 is absent. Again, “Prs. 1c-3, 4-7” indicates that in the first three areas the spots are paired, but single in the last four areas. “Split” has been explained. Sometimes a spot so clearly shows its origin from a pair, not quite blended into a single unit, that the expression “F. pr.” (fused pair) is used. The extension of spots of one series to meet another is indicated thus—under the heading Admarginal would be found “Pr. 1b to S.” and under Submarginal, the spot being single, “1b to A”; if the extension seems to be entirely on the part of the admarginals the entry under that head would not be followed by an entry under submarginals. Since these “maxima” and “minima” have been expressed as a result of examination of very many specimens it is thought that a definite statement of the range of variation in each form up to the present time may have an evolutionary interest for the future, should anyone at a later date attempt a similar task after a sufficiently long interval. It is obvious that some of the species here considered are in a highly variable state, e.g., *boisduvalii*, *sylvester*, *treitschkei* or *callithoe*. Some are apparently losing the spots as No. 136, *usipetes*, has done and Nos. 24-25, *wallacei*, also, and many forms, of *batesii* for example, have lost them on the upper surface.

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
1	<i>brunnescens</i> (Pl. 2, fig. 2)	♂ Holotype	Above	F. Small pr. 1b to S., small prs. 2-3	1b to A., 2: 5-9 (7 min.)	3 (incised externally): 10-11		
				H. Prs. 1c-6	Prs. 1c-3 (2 and 3 scarcely elongated), f.pr. 4, 5-6			
			Below	F. Pr. 1b, 2-3: small pr. 5	1b-2: tr. 4, 5-9, tr. 10	3-6: 10-11	+	
				H. 1b to S., prs. 1c-6	1b to A., prs. 1c-3, pr. 4, 5-6	1c-7	+	
		♂ Max.	Above	F. Prs. 1b-3	1b, small 2: 5-9, small 10	3 (large, incised externally): 10-11		
				H. Prs. 1c-6, 7	Prs. 1c-4 (very little elongated), 5-6			
			Below	F. Prs. 1b-3: prs. 5-6, 7	1b-2: 5-9	3 (large, hooked at base), 4-6: 10-11	+	
				H. 1b, prs. 1c-6, 7	1b, prs. 1c-4, 5-7	1c-7	+	
		♂ Min.	Above	F. Prs. 1b-3	2: 5-9	3: 10-11		
				H. Prs. 2-6	Prs. 2-4, 5-6			
			Below	F. Prs. 1b-3: trs. 5-6	1b-2: 5-9	3-4: 10-11		
				H. 1b, prs. 1c-6	1c, prs. 2-4, 5-6	1c-7	Trace	
		♀ Allotype	Above	F. Small prs. 1b-3	1b to A., 2: 5-9	3 (not incised), small 10-11		
				H. 1c to S., prs. 2-6	Pr. 1c (one to A.), prs. 2-3 elongated, short f.pr. 4, 5-6			
			Below	F. Pr. 1b to S., prs. 2-3: small prs. 5-6	1b to A., 2: 5-9	3, 4: 10-11	Minute	
				H. 1b and 1c to S., prs. 2-6	1b and pr. 1c to A., prs. 2-3 elongated, pr. 4 scarcely fused	1c-2 small: 4-7	Small	
2	<i>lilybaea</i>	♂ Type not designated						
		♂ Max.	Above	F. 1b, prs. 2-3: 5	1b-2: min. 4, 5-10	3: 10-11		
				H. Prs. 1c-6, 7	1c, prs. 2-3, split 4, 5-6			
			Below	F. 1b, prs. 2-3, 4, prs. 5-6, 7	1b, 2: min. 4, 5-9	3, small 4-6: 10-11	+	
				H. Prs. 1b-6, 7	1c, prs. 2-3, 4-7	1c-7	+	
		♂ Min.	Above	F. Sparse and irregular	1b-2: 5-8	3: 10		
				H. Prs. 2-6	1c, prs. 2-3, 4-6			
			Below	F. Sparse and irregular	1b-2: 5-8	3: 10	+	
				H. Prs. 2-6	1c, prs. 2-3, 4-6	1c: 7	Minute	
		♀ Type	Above	F. Prs. 1b-3	2: 5-6: 8-9	3: 10-11		
				H. Prs. 1c-6, linear 7	Tr.pr. 1c, prs. 2-3, 4-6			
			Below	F. Pr. 1b to S., prs. 2-3, trs. prs. 5-6, 7	Pr. 1b to A., 2: 5-6: 8-9	3, min. 4: 10-11	+	
				H. 1b, prs. 1c-6	1c, prs. 2-4, 5-6, tr. 7	1c, 2: trs. 4-6	+	
		♀ Max.	Above	F. Prs. 1b-3: trs. 5-6	Pr. 1b, 2: 5-10	3: 10-11		
				H. Prs. 1c-6, linear 7	Prs. 1c-3, f.pr. 4, 5-7			

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
3	<i>montrouzieri</i>	♀ Min.	Below	F. Prs. 1b-3, tr. 4, prs. 5-6, 7	1b to A., 2-3, tr. 4, 5-10	3-6 : 9-11	+
				H. 1b, prs. 1c-6, linear 7	Prs. 1c-4, 5-7	1c-7	+
			Above	F. Trs. 2-3	2 : 5-9		
				H. Tr. 1c, prs. 2-6	Prs. 2-3, f.pr. 4, 5-6		
		♂ Type	Below	F. Prs. 1b-3	2 : 5-9	3 : 10-11	+
				H. Prs. 1c-6	Prs. 1c-3, f.pr. 4, 5-7	1c-7 (3 on Rt. and 5-6 on Lt. min.)	+
			Above	F. Pr. 1b to S., prs. 2-3, trs. 5-6	Pr. 1b to A., 2 : tr. 4, 5-9 (7 and 9 min.)	3 : 10-11	
				H. Tr.pr. 1c ; prs. 2-6	Prs. 2-3, split 4, 5-6		
		♂ Max.	Below	F. Pr. 1b to S., prs. 2-3 : prs. 5-6, 7	Pr. 1b to A., 2 : tr. 4, 5-9	3-6 : 10-11	+
				H. 1b, prs. 1c-6, linear 7	1c, prs. 2-3, split 4, 5-7	1c-7	+
			Above	F. Prs. 1b-3, trs.prs. 4-5, tr. 6	Pr. 1b to A., 2 : 5-10	3 : 10-11	
				H. 1c, prs. 2-6, 7	Prs. 1c-3, split 4, 5-7		
		♂ Min.	Below	F. Pr. 1b to S., prs. 2-3, min. 4, prs. 5-7	Pr. 1b to A., 2 : min. 4, 5-9, tr. 10	Small 2, 3-6, 9-11	+
				H. 1b, prs. 1c-6, 7	Prs. 1c-4, 5-7	1c-8	+
			Above	F. Prs. 1b-2, 3	2 : 5-9 (7 min.)	3 : 10-11	
				H. Prs. 3-6	Pr. 3, f.pr. 4, 5-6		
		♀ Type	Below	F. F.pr. 1b, prs. 2-3 : trs. 5-6	1b to A., 2 : 5-9	3, tr. 4 : 10-11	Minute
				H. 1b, pr. 1c : prs. 3-6	2, prs. 3-4, 5-6	1c-2 : 5-7	Minute
			Above	F. Prs. 2-3 : tr. 5	2 : 5-9	3 very large : 10-11 large	
				H. Tr.pr. 1c, prs. 2-6, linear 7	Prs. 2-3, 4-7	7 shows from beneath	
		♀ Max.	Below	F. 1b, prs. 2-3 : small prs. 5-7	2 (larger than on upper side) : 5-9	3 very large, 4-6 : large 10-11	+
				H. 1b, prs. 1c-6, 7	1c, prs. 2-4, 5-7	1c-7	+
			Above	F. Prs. 1b-3, trs.prs. 4-5, tr. 6	1b to A., 2 : min. 4, 5-10	3 : 10-11	
				H. 1c, prs. 2-6, 7	Prs. 1c-3, split 4, 5-7	7	
		♀ Min.	Below	F. Pr. 1b to S., prs. 2-3, min. 4, prs. 5-6, 7	1b to A., 2 : min. 4 : 5-9, tr. 10	3-6 : 9-11	+
				H. 1b, prs. 1c-6, 7	Prs. 1c-4, 5-7	1c-8	+
			Above	F. Prs. 1b-2	2 : 5-8	3 : 10-11	
				H. Faint 4-5	Pr. 3, f.pr. 4, 5-6		
			Below	F. Prs. 1b-3 : pr. 6, 7	2 : 5-8	3, min. 4 : 10-11	+
				H. Minute 1b, prs. 1c-6	Prs. 2-3, 4-6, tr. 7	Minute 6-7	Minute

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell			
4	<i>eschschoitzii</i>	♂ Holotype	Above	F.	1b to S., prs. 2-3	1b to A., 2 : 5-9 (7 min.)	3 : 10-11			
				H.	Prs. 1b-6, 7	1b, prs. 1c-3, 4-7	7 shows from beneath			
			Below	F.	1b to S., prs. 2-3 : prs. 5-6, 7	1b to A., 2 : min. 4, 5-9	3-5 : 10-11	+		
				H.	1b to S., prs. 1c-6 (1c inner member to S.) 7	1b to A., prs. 1c-3 (1c inner member to A.), 4-7	1c-7	+		
		♂ Max.	Above	F.	Prs. 1b-3, min. 5-6	1b-2 : 5-10	3 : 10-11			
				H.	Prs. 1b-6, linear 7	Prs. 1b-3, 4-7	7 shows from beneath			
			Below	F.	1b to S., prs. 2-3, min. 4, prs. 5-6, 7	1b to A., 2 : small 4, 5-9	3-6 : 9-11	+		
				H.	Pr. 1b to S., prs. 1c-6, 7	1b to A., prs. 1c-3, f.pr. 4, 5-7	1c-7	+		
		♂ Min.	Above	F.	F.pr. 1b, pr. 2, 3	5-6 : 8-9	3 : trs. 10-11			
				H.	1b, prs. 1c-6	Prs. 1c-3, 4-6				
			Below	F.	F.pr. 1b, prs. 2-3 : pr. 5, min. 6	2 : 5-9	3 : small 10	Minute		
				H.	1b, prs. 1c-6	1b, prs. 1c-3, f.pr. 4, 5-7	Tr. 1c, 2 : 4 very small : 6 very small	Trace		
		♀ Allotype not designated								
		♀	Max.	Above	F.	Prs. 1b-3 : pr. 5, min. 6	1b to A., 2 : 5-10	3 : 10-11		
					H.	Prs. 1c-6, linear 7	Prs. 1c-3, f.pr. 4, 5-7			
				Below	F.	F.pr. 1b to S., prs. 2-7 (4 very small)	1b to A., 2 : min. 4, 5-11	3-11, also another spot in 10 base	+	
					H.	1b to S., prs. 1c-6, 7	1b to A., prs. 1c-3, f.pr. 4, 5-7	1c-7	+	
				♀ Min.	Above	F.	Prs. 1b-3	2 : 5-9	3 : 10-11	
						H.	Prs. 1c-6	Prs. 1c-3, 4-7		
					Below	F.	Prs. 1b-3 : prs. 5-6, 7	2 : 5-9	3 : 10-11	+
H.	1b to S., prs. 1c-6					1b to A., prs. 1c-3, 4-7	1c-7	+		
5	<i>lauensis</i>	♂ Holotype	Above	F.	Tr. 2	Small 2 : 5-6 : 8-9	3 small and blackened : trs. 10-11			
				H.	Prs. 1c-6	Prs. 1c-4, 5-6	7 shows from beneath			
			Below	F.	Prs. 1b-3 : min. 5	2 : 5-9	3 hooked at base, tr. 4 : tr. 6 : small 10-11			
				H.	Prs. 1c-6	1b, prs. 1c-4, 5-6, tr. 7	1c-7	Small		
		♂ Max.	Above	F.	Prs. 1b-3, 5	1b to A., 2 : 5-9	3 : small 10-11			
				H.	Prs. 1c-6, linear 7	Prs. 1c-4, 5-7				
			Below	F.	Pr. 1b to S., prs. 2-6, 7	Pr. 1b to A., 2 : 5-9	3, min. 4-5, small 6 : 10-11	Trace		
				H.	1b to S., prs. 1c-6, linear 7	1b to A., prs. 1c-3, 4-7	1c-7	Small		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
6	<i>distincta</i> (Pl. 2, fig. 3)	♂ Min.	Above	F. Tr. 2	2 : 5-6 : 8-9	3	
		H. Prs. 1c-6, linear 7	Prs. 1c-3, 4-6				
			Below	F. Prs. 1b-2, 3	1b-2 : 5-6 : 8, tr. 9	3 (ant-ext. part only)	
		H. Prs. 1c-6	1c, small prs. 2-3, f.pr. 4, 5-6				
		♀ Allotype	Above	F. Prs. 1b-3	1b, 2 : 5-6, tr. 7, 8-9	3 blackened : 10-11 small	
		H. Prs. 1c-6, linear 7	Prs. 1c-3, 4-6, tr. 7	7			
			Below	F. Prs. 1b-3 : prs. 5-6, 7	1b, 2 : 5-9	3, small 4 : small 6 : 10-11	Small
		H. 1b to S., prs. 1c-6, linear 7	1b to A., prs. 1c-3, 4-6	1c-6, large 7, linear 8	+		
		♀ Max.	Above	F. Prs. 1b-3 : 5	1b, 2 : 5-9	3 : 10-11 small	
		H. 1b, prs. 1c-6, linear pr. 7	Prs. 1c-3, 4-7				
			Below	F. Prs. 1b-3 : prs. 5-6, 7	1b to A., 2 : 5-9	3, small 4 : small 6 : 10-11	Trace
		H. 1b to S., prs. 1c-6, 7	1b to A., prs. 1c-4, 5-6 prs. barely fused, 7	1c-7	+		
		♀ Min.	Above	F. Prs. 1b-3	1b, 2 : 5-6 : 8-9		
		H. Prs. 1c-6, 7	Prs. 1c-3, 4-7				
			Below	F. Prs. 1b-3 : pr. 5, 6	2 : small 5-9	3 : trs. 10-11	
		H. 1b to S., prs. 1c-6, 7	1b to A., prs. 1c-4, small 5, 6	1c : 6-7	Trace		
		♂ Type not designated					
		♂ Max.	Above	F. Prs. 1b-4, tr. 5	2 : 5-9, tr. 10	3 : 10-11	
		H. Small prs. 1c-6, linear 7	Tr. 1b, prs. 1c-4, 5-7				
			Below	F. Prs. 1b-3, 4, prs. 5-6, 7	Small 2 : small 4, 5-9	Small 2, 3, 4-6, 10-11	Large
H. 1b to S., prs. 1c-6, linear 7	Prs. 1b-5, 6-7	1c-7	+				
♂ Min.	Above	F. Trs. 2-3	Small 2 : 5-9	3			
H. Prs. 1c-6	Prs. 1c-4, 5-6						
	Below	F. Prs. 1b-3 : pr. 5, 6	2 : 5-9	3-5			
H. 1b to S., prs. 1c-6	1b to A., prs. 1c-4	4-7	Very small				
♀ Holotype (H-S's figure)	Above	F. Prs. 2-3	2 : 5-9	Small 3 incised externally : small 10-11			
H. 2 : prs. 3-6	Small prs. 1c-4, 5-6						
	Below	F. 1b, prs. 2-3 : 5	Small 2 : 5-9	Small 3 incised externally, small 4-5 : 10-11			
H. Prs. 1c-6	Prs. 1c-4, 5-6	1c-7	Small				
♀ Max.	Above	F. Prs. 1b-3 : trs. 5-6	1b-2 : 5-10	3 : 10-11			
H. Tr. 1b, prs. 1c-6, linear 7	Tr. 1b, prs. 1c-4, 5-7						
	Below	F. Prs. 1b-3 : prs. 5-6, 7	1b-2 : 4-9	3-6 : 10-11	+		
H. 1b to S., prs. 1c-6	Trs. 1b-4, 5-6	1c-7	+				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
7	<i>lewini</i>	♀ Min.	Above	F. Trs. 2-3	2 : 5-6, tr. 7, 8-9	3 : 10-11	
				H. Small prs. 2-6	Small 4-6		
			Below	F. Prs. 1b-3 : pr. 5	1b to A. : 5-9	3-5 : 10-11	Trace
				H. 1b, prs. 1c-6	Minute 4-6	1c-2 : 4-7	Small
		♂ Holotype	Above	F. Pr. 1b to S., prs. 2-3 : trs. 5-6	Pr. 1b to A., 2 : min. tr. 4 on R., 5-9 (7 and 9 min.)	3 : 10-11	
				H. Tr.pr. 1c, prs. 2-6, min. 7	Prs. 2-3, split 4, 5-7		
			Below	F. Pr. 1b to S., prs. 2-3, small prs. 5-6, 7 (single on L., pr. on R.)	Pr. 1b to A., 2 : tr. 4, 5-9	3-6 : 10-11	+
				H. 1b, prs. 1c-6, 7	1c, prs. 2-3, split 4, 5-7	1c-7	+
		♂ Max.	Above	F. Pr. 1b to S., prs. 2-6	Pr. 1b to A., 2 : 4-9, tr. 10	3 : 9-11	
				H. 1b and pr. 1c to S., prs. 2-6 (some elongated to S.), linear 7	1b and pr. 1c to A., f.prs. 2-3, 4-7		
			Below	F. Pr. 1b to S., prs. 2-7	Pr. 1b to A., 2 (large) : 4-9 (4 arrow shaped)	3-6 : 9, 10-11	+
				H. 1b, pr. 1c to S., prs. 2-6, linear 7	1b, pr. 1c to A., f.prs. 2-4, 5-7	1c-7	+
		♂ Min.	Above	F. Prs. 1b-3	2 : 5-9	3 : 10-11	
				H. 1b, pr. 1c to S., prs. 2-6	1b, pr. 1c to A., f.prs. 2-3, 4-6		
			Below	F. Prs. 1b-3, trs. 5-6	2 : 5-9	3 : 10-11	
				H. 1b and pr. 1c to S., prs. 2-5, 6	1b and pr. 1c to A., f.prs. 2-3, 4-6	4-6	
♀ Allotype not designated							
♀ Max.	Above	F. 1b to S. large, prs. 2-3 : pr. 5, 6	1b to A., very large 2 : small 4, 5-9, tr. 10	3 very large : 10-11			
		H. 1b and pr. 1c to S., prs. 2-6, linear 7	1b and pr. 1c to A., f.pr. 2, pr. 3, 4-7				
	Below	F. 1b to S., prs. 2-3, 4, prs. 5-6, 7	1b to A., 2 : 5-9	Tr. 2, large 3, 4-6 : 9-11	+		
		H. 1b and pr. 1c to S., prs. 2-6, linear 7	1b and pr. 1c to A., prs. 2-3, 4-7	1c-7	+		
♀ Min.	Above	F. 1b to S., prs. 2-3 : min. 5	1b to A., 2 : 5-9	3 : 10-11			
		H. 1b and pr. 1c to S., prs. 2-6	1b and pr. 1c to A., f.prs. 2-3, 4-6				
	Below	F. 1b to S., prs. 2-3 : prs. 5-6	1b to A., 2 : 5-9	3, small 4 : 10-11	Small		
		H. 1b and pr. 1c to S., prs. 2-6	1b and pr. 1c to A., f.prs. 2-3, 4-6	1c-7 (small)	Trace		
8	<i>bourkei</i>	♂ Holotype	Above	F. Pr. 1b to S., prs. 2-3 : min. pr. 5, tr.pr. 6	Pr. 1b to A., 2 : 5-9	3 large : 10-11 large	
H. 1b to S., prs. 2-6	1b to A., pr. 1c, f.pr. 2, pr. 3, f.pr. 4, 5-6						

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
			Below	F. Pr. 1b to S., prs. 2-3 : small prs. 5-6, tr. 7	Pr. 1b to S., 2 : 5-9	3 large, 4 small : 10-11	+
				H. Prs. 1c-6	Pr. 1c, f.pr. 2, pr. 3, small pr. 4, 5-6	1c min. : 4-7	Small
			Above	F. Prs. 1b-3 : prs. 5-6, 7	1b to A., 2 : 5-9	3 : 10-11	
				H. 1b and pr. 1c to S., prs. 2-6, 7	1b and pr. 1c to A., prs. 2-3, 4-7		
			Below	F. Pr. 1b-3, tr. 4, 5-7	1b to A., 2 : 5-9	3, 4-6 : 10-11	Large
				H. 1b and pr. 1c to A., prs. 2-6, 7	Prs. 1b-3, 4-7	1c-7	+
			Above	F. Prs. 1b-3 : tr. 5	1b, 2 : 5-9		
				H. Prs. 1c-6	1b, prs. 1c-3, 4-6		
			Below	F. Prs. 1b-3 : pr. 5, 6	1b to A., 2 : 5-9	3, tr. 4 : trs. 10-11	
				H. Prs. 1c to S., prs. 2-6	1b, prs. 1c to A., prs. 2-3, 4-6	Minute 1c : min. 4-5	
			Above	F. 1b to S., small prs. 2-3 : 5	1b to A., 2 : 5-9	3 : 10-11	
				H. Prs. 1c-6	1b, prs. 1c-3, 4-7	7 shows from beneath	
			Below	F. 1b to S., prs. 2-3 : small prs. 5-6, 7	1b to A., 2 : 5-9	3 large, 4 small : 10-11	Small
				H. Prs. 1c-6	1b, prs. 1c-3, 4-7	1c-7	Small
			Above	F. Prs. 1b-6, 7	1b to A., 2 : 5-10	3 large : 10-11	
				H. Prs. 1c-6, linear 7	1b, pr. 1c, f.prs. 2-3, 4-7	7 shows from beneath	
			Below	F. Prs. 1b-7	1b to A., 2 : tr. 4, 5-10	3 large, 4-6 small : 10-11	+
				H. Prs. 1c-6, 7	Prs. 1b-3, 4-7	1c-7	+
			Above	F. Prs. 1b-3 : trs. 5-6	1b to A., 2 : 5-9	3 : 10-11	
				H. Prs. 1c-6	1b, prs. 1c-6		
			Below	F. Prs. 1b-3 : small prs. 5-6, 7	2 : 5-9	3 : 10-11	
				H. Prs. 1c-6	1b, prs. 1c-6, 7	1c : 4-6	+
			Above	F. 1b to S., prs. 2-3 : trs. 5-6	1b to A., 2 : 5-6 large, 7-9	3 large : 10	
				H. Large. Pr. 1c to S., prs. 2-6	Large. Pr. 1c to A., prs. 2-3 elongated, 4-6		
9	<i>walkeri</i> (Pl. 2, fig. 4)	♂ Holotype	Below	F. Pr. 1b to 3 : 5-6	1b to A., 2 : 5, large 6, 7-8, min. 9	3 very large, 4-6 min. : 10, tr. 11	Minute
				H. 1b and pr. 1c to S., prs. 2-6	1b and pr. 1c to A., prs. 2-3 elongated, f.pr. 4, 5-7	1c-7 min.	Minute
			Above	F. Prs. 1b-3, 4, prs. 5-6	1b to A., 2 : small 4, 5-9	3 large : 10-11 large	
				H. Prs. 1b and 1c to S., prs. 2-6, 7	Prs. 1b and 1c to A., prs. 2-3 elongated, 4-7	7 shows from beneath	
			Below	F. Pr. 1b to S., prs. 2-7, 8	Pr. 1b to A., 2 : small 4, 5-9	3, 4-6 : tr. 9, 10-11	Small
				H. Prs. 1b and 1c to S., prs. 2-6, 7	Prs. 1b and 1c to A., prs. 2-3 elongated, f.pr. 4, 5-7	1c-7	Small
			Above	F. Prs. 1b-3 : prs. 5-6, 7	1b to A., 2 : 5-9	3 : 10-11	
				H. 1b and pr. 1c to S., prs. 2-6, 7	1b and pr. 1c to A., prs. 2-3, 4-7		
			Below	F. Pr. 1b-3, tr. 4, 5-7	1b to A., 2 : 5-9	3, 4-6 : 10-11	Large
				H. 1b and pr. 1c to A., prs. 2-6, 7	Prs. 1b-3, 4-7	1c-7	+
			Above	F. Prs. 1b-3 : tr. 5	1b, 2 : 5-9		
				H. Prs. 1c-6	1b, prs. 1c-3, 4-6		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
10	<i>perryi</i>	♂ Min.	Above	F. Prs. 1b-3	1b, 2 : 5 : 8	3 : 10 min.		
		H. Prs. 1c-6		Prs. 1c-3, 4-6 (2-3 less elongated)				
		Below	F. Prs. 1b-3 : tr. 5	1b, 2 : 5-7	3, min. 4 : 10-11 small			
			H. Prs. 1c-6	Prs. 1c-3, 4-6 (2-3 less elongated)	2 : 5, min. 6	Trace		
		♀ Allotype not designated						
		♀ Max.	Above	F. Prs. 1b-3 : smaller prs. 5-6, tr. 7	Pr. 1b, 2 : 5-10	3 : 10-11 large		
		H. 1b and pr. 1c to S., prs. 2-6, linear 7		1b and pr. 1c to A., prs. 2-3, f.pr. 4, 5-7				
		Below	F. Prs. 1b-3, smaller prs. 4-7	Pr. 1b, 2 : small 4, 5-10	3, 4-6 : 9-11	+		
			H. 1b and pr. 1c to S., prs. 2-6, linear 7	Prs. 1b and 1c to A., prs. 2-3 (much elongated), 4-7	1c-7	+		
		♀ Min.	Above	F. Prs. 1b-3	Pr. 1b, 2 : 5-9 (7 and 9 min.)	3 : tr. 10		
		H. Prs. 2-6		Prs. 1c-3, 4-6				
		Below	F. Pr. 1b-3 : tr. 5	1b to A., 2 : 5-9	3 : 10-11			
			H. Prs. 2-6	Prs. 1c-3, 4-6	1c, min. 2 : 7	Minute		
		♂ Holotype	Above	F. Trs. 2-3	Small 2 : 5-6, tr. 7, 8-9	3 contracted, 10-11 very small		
		H. 2, prs. 3-6		Small, 1c, prs. 2-3, 4-6				
		Below	F. Minute 1b, prs. 2-3	Small 2 : 5-9	3 not contracted, trs. 4-5 on R. : 10-11			
			H. 1b, prs. 1c-6. All minute	Very small. 1b, prs. 1c-3, split 4, 5-6	Minute 6			
		♂ Max.	Above	F. Prs. 1b-3 : trs. 5-6	1b to A., 2 : 5-9 (7 min.)	3 : 10-11		
		H. Prs. 1b-6, 7		Very small. Prs. 1b-3, 4-7				
		Below	F. Prs. 1b-3 : prs. 5-6, 7	1b to A., 2 : 4-9	3, min. 4-6 : Small min. 9, 10-11			
			H. 1b, prs. 1c-6, 7	1b, prs. 1c-4, 5-7	1c-7	Small		
♂ Min.	Above	F.						
H.								
Below	F.		10-11					
	H.		1c : 4-6	Minute				
♀ Allotype not designated								
♀ Max.	Above	F. 1b, prs. 2-3	2 : 5-9 (7 min.)	3 : 10-11				
H. Prs. 2-5, 6		Prs. 1c-3, 4-6						
Below	F. 1b, prs. 2-3 : prs. 5-6, 7	Minute 1b, 2 : 5-9	3, min. 4-6 : Small 10-11					
	H. Prs. 1c-6	Prs. 1c-3, 4-7	1c-7	+				
♀ Min.	Above	F.	Tr. 2	Tr. 3				
H.								
Below	F. Minute pr. 2	2 : 5-9	Small 3 : 10-11	Minute				
	H. 1c, min. prs. 2-3	1c, prs. 2-3, 4-5, tr. 6	Tr. 2 : 5-6					

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
11	<i>doretta</i>	♂ Type	Above { F.		Tr. 5, min. 6-7		
			H.				
			Below { F.		3-8	2 (very faint),	+
			H.	Prs. 4-5, 6	4-7	3-4 : 6 1c-6 (6 large)	+
		♂ Max.	Above { F.		Tr. 5, min. 6-7		
			H.				
			Below { F.	Trs. 3-4 : 7	2-8	2-6 : tr. 10	+
			H.	Prs. 4-6	4-7	1c-7	+
		♂ Min.	Above { F.				
			H.				
			Below { F.		6-7	Small 3-4	Minute
			H.		Small 4-6	Minute 2-4 : 6	+
		♀ Type	Above { F.		3-7		
			H.	Faint pr. 6, 7	4-6		
	Below { F.		Minute 1b, 2-6	Large 2, 3-4 : 6	+		
	H.	Prs. 1c-6	4-7	1c-7 (2 and 6 large)	+		
Another ♀	Above { F.		Small 3-7				
	H.	Prs. 4-5, small 6	Small 4-7				
	Below { F.		1b-6	2-6	+		
	H.	1b, prs. 1c-6	4-7	1c-7	+		
12	<i>macleari</i>	♂ Holotype	Above—F. H.				
			Below { F.		Minute 3-6	2-3	+
		H.	Large prs. 4-6	4-6	Minute 2-5, 6	Small	
		♂ Max.	Above—F. H.				
			Below { F.		Small 2, 3-4 : 6-7	2-4	+
		H.	Prs. 2-6	4-6	1c-7	+	
		♂ Min.	Above—F. H.				
			Below { F.			3-4	+
		H.	Prs. 5-6	5-6	Minute 3-6	Minute	
		♀ Allotype not designated. Only one female specimen seen.					
13	<i>nobilis</i>		Above—F. H.				
			Below { F.		Minute 2-4	2-4	+
		H.	Pr. 6	5-7	3-6	+	
		♂ Holotype	Above { F.			3	Large
			H.				
			Below { F.		Small 4-8	2-4 : small 6	Large
			H.		4-6	1c-6 (4-5 min.)	+
		♂ Max.	Above { F.		3-7	3	Large
H.			4-6				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
			Below	{ F. H. 2, prs. 3-6	2-8 4-7	2-4 : 6 1c-7	Large +
		♂ Min.	Above	{ F. H.			Small
			Below	{ F. H. Tr. 6	Small 3-4 : small 6-7 4-6	3-4 3-6	+ +
		♀ Allotype	Above	{ F. H.		Small 3 : small 6 Minute 3 on R. : 6	Large
			Below	{ F. H. Pr. 5, 6. Single 4 on L.	2-7, min. 8 4-6, small 7	Minute 2, 3, min. 4 1c, 2, min. 3, tr. 4 on R. : large 6	Large Large
		♀ One other	Above	{ F. H.	4-7	3-4 : 6 Small 3-4 : 7	Large
			Below	{ F. H. Minute pr. 5, 6	Small 3-8 4-6	2-4 : 6 1c-4 : 6-7	Large Large
14	<i>lugens</i>	♂ Holotype	Above	{ F. H.	Small split 1b, 2-9 1b, prs. 1c-3, 4-6		
			Below	{ F. Tr. 2 H. 1b to S. : trs. 4-6	Small split 1b, 2-9 Pr. 1b (one to A.), prs. 1c-3, 4-6	Minute 2-3 Very small 1c-4, tr. 5, small 6	Small Very small
		♂ Max.	Above	{ F. Prs. 1b-4, 5-6 H. 1b, prs. 1c-6, 7	Pr. 1b (one to A.), 2-10 Prs. 1b-3, 4-6	10, tr. 11	
			Below	{ F. Prs. 1b-6 H. 1b, prs. 1c-6, 7	Pr. 1b, 2-9 1a, prs. 1b-3, 4-6, tr. 7	2-4, tr. 5 : 10 1c-7	+ +
		♂ Min.	Above	{ F. H.	2-9 Prs. 1b-3, 4-6		
			Below	{ F. 2-6, irregular H. 1b, pr. 1c : 3, prs. 4-5, 6	2-9 Prs. 1b-3, 4-6		Trace Very small
		♀ None seen					
15	<i>misagenes</i>	Type not available					
		♂ Max.	Above	{ F. Small prs. 1b-5 H. 1b to S., prs. 1c-6	F.prs. 1b-2, 3-10 Prs. 1b-3, 4-6, tr. 7		
			Below	{ F. Prs. 1b-6, 7 H. 1b to S., prs. 1c-6	Pr. 1b, 2-10 Prs. 1b-5, 6	2-3, tr. 4 2-6	Trace +
		♂ Min.	Above	{ F. Pr. 1b, tr. 2 H. Small prs. 4-5	Small 1b, 2, 3-9 1b, prs. 1c-3, 4-6		
			Below	{ F. H. 1b to S., prs. 1c-5, 6	Small 2-9 1b to A., prs. 1c-3, 4-6	2-3 2-3	Trace +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
16	<i>wernerii</i>	♀ Max.	Above {	F. Small prs. 1b-5	1a, 1b-10		
				H. Prs. 1b-6, 7	1b to A., prs. 1c-3, 4-7 (also in 1c a short pair along interneural fold)		
			Below {	F. Prs. 1b-6	F. pr. 1b, 2-10	2-6 : 9-10	+
				H. 1b to S., prs. 1c-6	Prs. 1b-3, 4-6	2-7	+
		♀ Min.	Above {	F.	1b-9, tr. 10		
				H. Irregular 1b-6	1b, prs. 1c-3, 4-6		
			Below {	F. Small pr. 1b	Small 2, 3-9	2, tr. 3	Trace
				H. 1b, prs. 1c-5, 6	1b, prs. 1c-3, 4-5	Minute 4-6	Trace
		♂ Holotype	Above {	F. Minute 1b-4	Minute 1b, 2-8	2-6 : 10	+
				H. 1c, prs. 2-5, tr. 6	1c, prs. 2-3, 4-6		
			Below {	F. Irregular 1b-6	Minute 1b, 2-8, tr. 9	2-6 : tr. 8, 9-11	+
				H. 1b, prs. 1c-6	1c, prs. 2-3, 4-6	1c-7	+
		♂ Max.	Above {	F. Prs. 1b-2, 3-4	Pr. 1b, 2-9	Streak 1b, 2-8 : 10-11	+
				H. Prs. 1c-5, 6	Prs. 1c-3, 4-6, tr. 7		
			Below {	F. Irregular 1b-6	Pr. 1b, 2-9	Streak 1b, 2-6 : trs. 8-9, 10	+
				H. 1b, prs. 1c-6, 7	Prs. 1c-3, 4-7	1c-7	+
		♂ Min.	Above {	F.	1b-8	Tr. 3 : small 10	
				H. Small prs. 4-5, 6	Small prs. 1c-3, 4-6		
			Below {	F.	1b-8	2-4 : 6 : tr. 10	Small
				H. 1b, small prs. 2-5, 6	1c, small prs. 2-3, 4-6	Tr. 1c, 2-3, trs. 4-5, 6	Minute
		♀ Allotype	Above {	F.	1b-9	Streak 1b, 2-6 : 10	+
				H. 1c : prs. 4-5, 6	Prs. 1c-3, 4-7		
			Below {	F.	1b-9	2-6 : 8-10	+
				H. 1b, prs. 1c-5, 6	Prs. 1c-3, 4-7	1c-7	+
		♀ Max.	Above {	F. Prs. 1b-6	Pr. 1b, 2-9	Streak 1b, 2-6 : 10	+
				H. Prs. 1c-6	Prs. 1c-3, 4-7	2-3 (4-5 show from beneath), 6-7	Shows from beneath
			Below {	F. Prs. 1b-7	Pr. 1b, 2-9	Streak 1b, 2-10	+
				H. 1b, prs. 1c-5, 6	Prs. 1c-3, 4-7	1c-7	+
		♀ Min.	Above {	F.	1b-8, tr. 9	Tr. streak 1b, 2-3, small 4-5, 6 : 10	+
				H. Irregular, 2-7	Prs. 1c-3, 4-6, tr. 7		
			Below {	F. Trs. 1b-2	1b-9	Streak 1b, 2-6 : 9-10	+
				H. 1b, prs. 1c-5, 6	Prs. 1c-3, 4-7	1c-7	+
17	<i>jennessi</i> (Pl. 4, fig. 5)	♂ Holotype	Above {	F.	2-9		
				H.	Trs. 4-5		
			Below {	F.	8	2-4	Small
				H.		1c-7	small

No.	Name	Example	Wings	Admarginals	Submarginals	Disicals	Cell
18	<i>insulicola</i>	♀ Allotype	Above	F. Irregular 1b-6	1b-9, tr. 10	10	
				H.		6 shows from beneath	
			Below	F. Irregular	Minute 1b, 2-9	1b-6 : min. 9, 10-11	
				H.		1c-7	+
		Another ♀	Above	F.	Large 4-7, 8, tr. 9		
				H.			
			Below	F.	Diffuse white scaling 3-5, spots 6-8	Large 2, small 3	Small
				H.	Minute 2-6		Small
		♂ Holotype	Above	F.	3-6	Trace streak 1b : 3, min. 4	Large
				H.	4-6		
			Below	F.	2-6, min. 7-8		Large
				H. Minute 1c and pr. 2, prs. 3-6	4-6	1c-7 (4-5 very small)	Large
		♂ Max.	Above	F.	Trs. 3-6 : tr. 8	Streak 1b, tr. 2, small 3-4 : tr. 6	Large
				H.	4-6		
			Below	F. Minute 3 : tr. 6	Minute 2, 3-8	Streak 1b, tr. 2, 3-6	Large
				H. 2, prs. 3-5, 6	4-6	1c-7	+
		♂ Min.	Above	F.	Trs. 5-6	Tr. streak 1b : small 3	+
				H.			
			Below	F.	Minute 4-6	Tr. streak 1b, small 2-3	+
				H. Trs. 4-6	Minute 4-6	Minute 1c, 2, min. 3 : min. 7	+
		♀ Allotype	Above	F.	Small 4-6	Elongated 1b : 3-4 : 6	Large
				H. Faint and irregular	4-6	1c-3, small 4-5, 6-7	
			Below	F.	3-6 : min. 8	Streak 1b, 2-4, min. 5-6	Large
				H. 1c, prs. 2-5, 6	4-7	1c, 2, small 3-4, 5-7	Large
		♀ Max.	Above	F. Ft.pr. 3, prs. 4-5, 6	1b large, elongated 2-8, tr. 9 on R.	Streak 1b, 2-8, trs. 9-10	Large with small accessory
				H. Prs. 2-5, 6	4-7	1c-7	Large
			Below	F. Prs. 1b-6, 7	1b-8	Streak 1b, 2-4 : 6	Large
				H. Prs. 1c-6, 7	4-7	1c-7	Large
		♀ Min.	Above	F.	Minute 4-6	Streak 1b reduced to oval spot, trs. 2-4	+
				H. Trs. 4-6	5-6	Tr. 1c, 2-3, min. 4	Small
			Below	F.	2-6	Small streak 1b, 2-4 : 6	Large
				H. Prs. 4-5, 6	Tr. 4, 5-6	1c-3 : 6-7	Large
19	<i>cerberus</i>	♂ Holotype	Above	F.	Tr. 3-6		
				H.			
			Below	F.	3-6 : min. 8	2-4 : 6	+
				H. Irregular	Minute 4, 5-6	2-6	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
	♂ Max.	Above	{ F.	Faint trs. 3-6	Tr. 2, 3-7, tr. 8	Small 3	+	
			{ H.	Trs. 5-6	Small 4-6			
		Below	{ F.	Minute 1b, prs. 1c-6, 7	1b-8	2-4, min. 5, 6	+	
			{ H.	1b, prs. 1c-6, 7	3-6 (or, 4-7)	1c-7	+	
	♂ Min.	Above—F. H.						
		Below	{ F.		6	2-4	Small	
	{ H.			4-6	2-3, trs. 4-5, 6	Minute		
	♀ Allotype	Above	{ F.		2-8	Small 3		
			{ H.	Prs. 4-6	4-6			
		Below	{ F.	Prs. 1b-2, 3: prs. 5-6	1b-8, min. 9	Large 2, 3-6	Small	
			{ H.	Prs. 1c-6, linear 7	4-6, min. 7	1c-7	+	
	♀ Max.	Above	{ F.	Trs. 2-3	2-8	Small 3		
			{ H.	Prs. 1c-6	4-7	7		
		Below	{ F.	Prs. 1b-7	1b-8	2-4, min. 5	Large	
			{ H.	1b, prs. 1c-6, 7	2, pr. 3, 4-7	1c-7	+ with accessory	
	♀ Min.	Above—F. H.						
		Below	{ F.		3: 5, min. 6	2-4	Trace	
			{ H.	Trs.	4-6	2-6	+	
20 <i>subpunctata</i>	♂ Holotype	Above—F. H.						
		Below	{ F.		Minute 2-6: 8	Small 2-4: 6	+	
			{ H.		Minute 5-6	2-7	+	
	♂ Max.	Above—F. H.						
		Below	{ F.		Minute 2-6: 8	Small 2-4: 6	+	
	{ H.			Minute 5-6	2-7	+		
	♂ Min.	Above—F. H.						
		Below	{ F.		Tr. 3	2-4: 6	+	
	{ H.				2-3, min. 4, 5-6	Small		
	♀ Allotype not designated							
	♀ Max.	Above	{ F.		2-7			
			{ H.	Ft. prs. 4-5, 6	4-6			
		Below	{ F.	1b, prs. 2-6, 7	1b-8	2-4: 6	+	
			{ H.	1b, prs. 1c-6	4-7	1c-7	+	
	♀ Min.	Above	{ F.		Minute 3: 5-6			
			{ H.	Trs. 4-6	4-6			
		Below	{ F.	Trs. 3-5	2-6: min. 8	2-3, min. 4: 6	+	
			{ H.	Small prs. 2-6	4-6	1c-7	+	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
21	<i>griseitincta</i>	♂ Holotype not designated					
		♂ Max.	Above { F. H.		2-6 5-6		
			Below { F. H.	3, prs. 4-5, 6	1b-8 4-7	Streak 1b, 2-6 (5 min.) 1c-7	+ +
		♂ Min.	Above { F. H.		3-6 5-6		
			Below { F. H.		2-6 4-6	2-4 2-6	+ +
		A single ♀	Above { F. H.		2-6 5-6		
			Below { F. H.	Prs. 4-5, 6	2-7 2, pr. 3, 4-6, min. 7	2-4 2-7	+ +
22	<i>obscura</i>	♂ Holotype	Above—F. H.				
			Below { F. H.		2-8 (2 and 8 min.) 4-7	4-6 Small 2-5, 6	
		♂ Max.	Above { F. H.		2-8 (2 and 8 min.) 5-6		
			Below { F. H.	1c, prs. 2-6, 7	Min. 1b, 2-7, min. 8 Small prs. 2-3, 4-7	Tr. 3, 4-6: small 10 Minute 1c, 2-7	Very small + with accessory
		♂ Min.	Above—F. H.				
			Below { F. H.		3-8 (3 and 8 min.) 4-7	Small 4 2-6	Very small Small
		♀ Allotype	Above { F. H.		Faint 6-7 Faint 5-7		
			Below { F. H.	2-3, prs. 4-5, 6	3-7, min. 8 Minute 3, 4-7	3-6: 10 1c-7 (1c and 7 small)	Small +
		One other ♀	Above { F. H.		5-7		
			Below { F. H.	1c, prs. 2-6	2-8 Prs. 2-3, 4-7	2-6: tr. 10 1c-6	+ +
23	<i>eboraci</i>	♂ Holotype	Above { F. H.		Minute 4-7		
			Below { F. H.	1c: 3 (pr. on L., single on R.), 4-6	2-8 2, pr. 3, 4-7	4, 5 narrow, 6 large 1c-6, large 7	Minute large +
		♂ Max.	Above { F. H.		Minute 4-7		
			Below { F. H.	1c, prs. 2-6	2-8 2, pr. 3, 4-7	2-4, tr. 5, 6 1c-6, large 7	+ +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
24	<i>melia</i>	♂ Min.	Above—F. H.				
			Below { F. H. Tr. 6		Small 3-6 Minute 4, small 5-6	4, trs. 5-6 2-6	Minute +
		♀ Allotype	Above { F. H.		6-7 Tr. 5, small 6		
			Below { F. H. 1c : 4-6		2-8 2, pr. 3, 4-7	Minute 3, 4-6 : tr. 10 1c-7	+
		♀ Max.	Above { F. H.		Minute 4 : 6-7 Tr. 5, small 6		
			Below { F. H. 1c, prs. 2-6		1b-9 Prs. 2-3, 4-7	3-6 : faint 9-10 1c-7	+
		♀ Min.	Above—F. H.				
			Below { F. H. Traces		2-8 4-7	4 : 6 2-6	Minute +
		♂ Holotype	Above—F. H.				
			Below { F. H.			Minute 2-4, tr. 5 on L.	Minute
		♂ Max.	Above—F. H.				
			Below { F. H.			2-6	+
25	<i>catana</i>	♂ Min.	Above—F. H.				
			Below { F. H.			Minute 3 on R. only	
		♀ Allotype not designated					
		♀ Max.	Above—F. H.				
			Below { F. H.		Tr. 2	2-6, streaks	Small
		♀ Min.	Above—F. H.				
			Below { F. H.			2-4, streaks	
		♂ Holotype	Above—F. H.				
			Below { F. H.			Minute 3-5	Minute
		♂ Max.	Above—F. H.				
			Below { F. H.			2-6	+ with small accessory
		♂ Min.	Above—F. H.				
			Below—F. H.				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Max.	Above—F. H.				
			Below { F. H.		2	2-6	+
		♀ Min.	Above—F. H.				
			Below—F. H.				
26	<i>auritincta</i>	♂ Holotype	Above—F. H.				
			Below { F. H.			Large 2, 3-4 : tr. 6 1c-7	+
		♂ Max.	Above—F. H.				
			Below { F. H.			Large 2, 3-4, tr. 5, 6 1c-7	+
		♂ Min.	Above—F. H.				
			Below { F. H.			Small 2-4 : tr. 6 1c-7	+
		♀ Unknown					
27	<i>trobriandensis</i>	♂ Holotype	Above—F. H.				
			Below { F. H.			2-4 2-6	+
		♂ Max.	Above—F. H.				
			Below { F. H.			2-4 1c-7	+
		♂ Min.	Above—F. H.				
			Below { F. H.			2, small 3-4 2, small 6	Minute Small
		♀ Allotype	Above { F. H.			Tr. 1b : min. 3 Ft.tr. 4-5, 6	Small
			Below { F. H.			2-4 : small 10 1c, 2-6, tr. 7 R. only	Large Large, with accessory
28	<i>nanum</i>	♂ Holotype	Above—F. H.				
			Below { F. H.			Tr. 2-3 2, min. 3-4, 5-6, linear 7	Small +
		♀ Unknown					
29	<i>rotunda</i>	♂ Type not available					
		♂ Max.	Above—F. H.				
			Below { F. H.			2-4 2-6	+ with accessory + with accessory

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♂ Min.	Above—F. H.				
			Below { F. H.			3-6	+
		♀ Type not available					
		♀ Max.	Above { F. H.		Faint 3 : 6-7		
			Below { F. H.			2-4 1c-7	+ Large
		♀ Min.	Above—F. H.				
			Below { F. H.			Tr. 2, small 3, tr. 4 2-6	+
30	<i>belia</i> (after the figures by Waterhouse & Lyell)	♂ Holotype	Above { F. H.		Faint indications 1a-8, spots 9-10 Faint indications prs. 1c-3, and of small prs. 4-5		
			Below { F. H.		Faint indications 1c-8, spots 9-10 Faint prs. 1c-6, 7	Small linear 2-4 2-6	Trace +
		♀ Allotype	Above—F. H.				
			Below { F. H.			2-4 2-6	+ +
31	<i>resarta</i> (Pl. 5, fig. 5)	♂ Type not designated					
		♂ Max.	Above { F. Pr. 1b to S., prs. 2-4, 5-6 H. 1b to S., prs. 1c-5 to S., pr. 6	Minute 1A, pr. 1b to A., f.prs. 2-6, 7-10 Prs. 1b-5 to A., f.pr. 6			
			Below { F. 1a, prs. 1b-6, 7 H. Prs. 1b-6 fused to S.	F.prs. 1b-6, 7-10 Prs. 1b-6 fused to A.	2-6 1c-7	Duplicated Large, with accessory	
		♂ Min.	Above { F. No spots, but a paler border H.	Faint prs. 1c-3, tr. 4			
			Below { F. H.			Trace Small 3-5, tr. 6	Minute
		♀ Holotype	Above { F. H. Pr. 1c to S., prs. 2-5, 6	1b-11, faint Prs. 1b-5			
			Below { F. Pr. 1b to S., prs. 2-4 H. Pr. 1c to S., prs. 2-5, 6	Pr. 1b to A., prs. 2-3, f.prs. 4-6, 7-11 Prs. 1b-5	2-3, min. 4 2-3 : 5-7	Minute +	
		♀ Max.	Above { F. 1a-4 to S., pr. 5 (half to S.), pr. 6 H. Prs. 1b-5 completely Pr. 6 separate, single 7	1a to A., f.prs. 1b-6, 7-10, tr. 11 fused with S1b-5, Pr. 6 separate			

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell		
32	<i>kungana</i> (Pl. 5, figs. 1, 4)	♀ Min.	Below	F.	Pr. 1b to S., prs. 2-7	1a. f.prs. 1b-6, 7-10, tr. 11	2-6	Duplicated	
				H.	Prs. 1b-5 completely fused with S. Pr. 6 separate	1b-5, Pr. 6 separate	1c-7	Duplicated	
			Above	F.		S. show as 'ghosts'			
				H.		S. show as 'ghosts'			
			Below	F.		S. show as 'ghosts'	Minute 2-3	Minute	
				H.	A. show as 'ghosts'	S. show as 'ghosts'	Small 2-6	Small	
			♂ Holotype and paratype	Above	F.		1b-9		
					H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, small 6		
		Below		F.	Prs. 1b-2, pr. 3 on R., single 3 on L., trs. 4-6	1b-8	Minute 2, 3		
				H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, min. 6	Minute 2-6		
		♀ Allotype		Above	F.		1b-9		
					H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, small 6		
				Below	F.	Prs. 1b-2 to S., 3	1b-2 to A., 3-8	1b two long streaks, 2-4	Trace
					H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, small 6	Minute 2-6	Trace
		♀ Paratype A	Above	F.		1b-9			
				H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, small 6			
			Below	F.	Irregular traces	1b-9	1b single long streak, 2-3		
				H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, small 6	Minute 2-4 : 6		
		♀ Paratype B	Above	F.		1b-9			
				H.	Pr. 6	Prs. 1b-3, f.prs. 4-5, small 6			
Below	F.		Irregular traces	1b-9	1b single short streak : 3				
	H.		Pr. 6	Prs. 1b-3, f.prs. 4-5	2-4				
33	<i>honestia</i> Series A. More spotted. (Pl. 6, figs. 1, 5)	♂ Type not designated							
		♂ Max.	Above	F.		Double streak 1b, 2-6 : 9-10	Large		
				H.					
		Below	F.		2-6 : 9-10	Split			
			H.		Pr. 1c, 2-7	Large			
		♂ Min.	Above	F.		Streak 1b short, tr. 2, small 3	Trace		
				H.					
		Below	F.		2-5, tr. 6	Small			
			H.		1c-6	+			
		♀ Type	Above	F.		Doublestreak 1b, small 2, 3-5, tr. 6 : 10	Large		
				H.		Faint 6			
		Below	F.		Doublestreak 1b, 2-6 : tr. 10	Large			
H.			1c-7	Large with accessory					

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Max.	Above { F. H.		Small 5-6 : 8, tr. 9	Streak 1b double, large 2-6 : 9, 10	Large with two accessory streaks
			Below { F. H.			2-6 : 9, 10	Large
		♀ Min.	Above { F. H.			Streak 1b single : 3-4	+ faint
			Below { F. H.			2-6 1c-7	+ +
	Series B. Less spotted	♂ Max.	Above { F. H.			Streak 1b, tr. 2, 3-6 : tr. 9, small 10	+
			Below { F. H.			2-6 : 9-10 1c-6	Split +
		♂ Min.-	Above—F. H.				
			Below { F. H.			2-4, tr. 5 Minute 2-6	Small Minute
		♀ Max.	Above { F. H.			Tr. streak 1b, 2-6 : 9-10	Large, split
			Below { F. H.		Minute 5-6	2-4, trs. 5-6 Streak 1b, pr. streaks 1c, large 2-7	+ Large
		♀ Min.	Above—F. H.				
			Below { F. H.			2-6 : tr. 10 1c-6, tr. 7	Small +
34	<i>woodfordi</i> (Pl. 7, figs. 1, 5)	♂ Holotype	Above { F. H.	Prs. 4-5	Faint pr. 1b, prs. 1c-2, small pr. 3		
			Below { F. H.	Faint prs. 1c-3, prs. 4-5		2-4, trs. 5-6 Faint 1c, 2-6	Minute +
		♂ Max.	Above { F. H.	Prs. 4-5	Prs. 1b-3, small pr. 4, tr. 5		
			Below { F. H.	Prs. 1c-5		2-6 : trs. 9-10 Trs. 1c-7	+ with accessory +
		♂ Min.	Above { F. H.		1b, prs. 1c-2, pr. 3		
			Below { F. H.			2-5, tr. 6 1c-7	Trace +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
35	<i>leucacron</i> (Pl. 8, fig. 1)	♀ Allotype	Above { F. H.	Irregular 2-5		Show through faintly	
			Below { F. H.				
		♀ Max.	Above { F. H.	Faint prs. 4-5		Trs. 3-4 Faint 2-6	Trace Trace
			Below { F. H.				
		♀ Min.	Above—F. H.		2-8	2-6 : trs. 9-10 1c-7	Large Large
			Below { F. H.				
		♂ Holotype	Above—F. H.			Small 2-4 Minute 2, small 3, 4-6	Trace +
			Below { F. H.				
		♂ Paratype	Above { F. H.		Pr. 1c, trs. 2-4	Small 2-4 Minute 2, small 3, 4-6	Small Small
			Below { F. H.				
		♀ Unknown					
36	<i>coffea</i>	♂ Ne-allotype	Above—F. H.			3-4 1c-6, tr. 7	
			Below { F. H.				
		♂ Max.	Above—F. H.			Small 2-3, 4, tr. 5, 6 : min. 10 1c-6, tr. 7	+ +
			Below { F. H.				
		♂ Min.	Above—F. H.			3 Small 2, min. 3-4 : tr. 6	
			Below { F. H.				
		♀ Holotype	Above { F. H.	Pr. 1b	Faint 1b Faint 5-6	2-4 : 6	+
			Below { F. H.				
		♀ Max.	Above { F. H.	Pr. 1b	Faint 1b Faint 5-6	2-4 : 6	
			Below { F. H.				
		♀ Holotype	Above { F. H.	Faint prs. 1b-2 Faint 1c, prs. 2-6	Minute 2-3 : 5-6 : 8 Small 4-7	2-4 : tr. 9, 10 2-6, linear 7	+ +
			Below { F. H.				
		♀ Max.	Above { F. H.	Pr. 1b	Faint 1b Faint 5-6	2-4 : 6	
			Below { F. H.				
		♀ Holotype	Above { F. H.	Faint prs. 1b-2 Faint 1c, prs. 2-6, linear 7	2-3 : 5-8 4-7	2-4. min. 5-6 : large 1c-7	+ Large
			Below { F. H.				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above—F. H.				
			Below { F. H.			Small 2-3 (or, 3-4) Minute 2 : 4-6	
37	<i>diadema</i>	♂ Ne-allotype	Above { F. H. 1b to S., prs. 1c-5		Minute 3-4, larger 5-6, 7-8 Prs. 1b-3, 4-5		
			Below { F. H. 1b to S., prs. 1c-5		Minute 3-4, larger 5-6, 7-8 Prs. 1b-3, 4-5	Minute 3-4 : tr. 6 Small 2-6	Minute
		♂ Max.	Above { F. prs. 1b-2, others irregular H. 1b, prs. 1c-5		Tr. 2, ft. 3, 4-9 Prs. 1b-3, 4-5		
			Below { F. Prs. 1b-3, tr. 4, prs. 5-6 H. Prs. 1b-5, 6		Small 2-4, 5-8, tr. 9 Prs. 1b-3, 4-6	Small 3-4 : tr. 6 : 10 2-7	+ +
		♂ Min.	Above { F. H.		5-8		
			Below { F. H. 1b, prs. 1c-5		5-8 1b, prs. 1c-3, 4-5	Tr. 5 one side only	Trace
		♀ Holotype	Above { F. Tr. pr. 1a H. 1b and pr. 1c to S., prs. 2-6		Tr. 1b, ft. 2, 3-8 Prs. 1b and 1c to A., prs. 2-3, 4-6	10	
			Below { F. Irregular 1b-6 H. Large 1b and pr. 1c to S., prs. 2-6		2-9 Prs. 1b and 1c to A., 2-6 prs. 2-3, 4-6	2-4 : tr. 6 : 10	+ Minute
		♀ Max.	Above { F. Prs. 1b-5, 6 H. Large 1b and pr. 1c to S., prs. 2-6, 7		Tr. 1b, 2-10 Prs. 1b and 1c to A., prs. 2-3, 4-6		
			Below { F. Large prs. 1b-6, 7 H. 1b and pr. 1c to S., prs. 2-6, 7		2-10 Large prs. 1b and 1c 2-7 to A., prs. 2-3, 4-6	2-4 : 10	+ +
		♀ Min.	Above { F. H.		3-8		
			Below { F. H. 1b, prs. 1c-4, 5		3-8 1b, prs. 1c-3, 4-5	Minute 2-3 : 6	Minute
38	<i>macgregori</i>	♂ Holotype	Above { F. H.		Pr. 1b, 2-3, tr. 4, 5-7 Prs. 1b-3, 4, tr. 5		
			Below { F. H. Pr. 1c (one to S.) : 4-5		Minute 1b, 2-3, tr. 4, Short 1b 5-7 Prs. 1b-3, 4-5, min. 6	Tr. 2, small 3-6	Trace
		♂ Max.	Above { F. H.		Small 1b-7, min. 8 Prs. 1b-3, 4-5		
			Below { F. H. 1b to S., prs. 1c-2, 3, prs. 4-5, 6		1b-8 (4 min.), tr. 9 Prs. 1b-3, 4-6, small 7	Minute 1b : 3-4 Streak 1b, 2-6	Minute Small

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
39	<i>samaraina</i> (Pl. 4, fig. 1)	♂ Min.	Above { F. H.		Tr. 5 one side, small 6 Prs. 1b-3, small 4, tr. 5		
			Below { F. H. 5		Minute 5-8 Prs. 1b-3, 4-5, tr. 6	2-3 : 6	
		♀ Allotype not designated					
		♀ Max.	Above { F. H. Prs. 5-6		1b-9 Prs. 1b-3, 4-6		
			Below { F. Pr. 1b H. Prs. 1b-2 : pr. 5, 6		1b-9 Prs. 1b-3, 4-6	Streak 1b, 2-3, min. 4 2-6	+ +
		♀ Min.	Above { F. H. Irregular traces		1b-3, tr. 4, 5-8 Prs. 1b-3, 4-6		
			Below { F. H. Prs. 1c-5 (1b broken away)		1b-3, tr. 4, 5-8 Prs. 1b-3, 4-6	2-3, min. 4 2-6 (4-5 min.)	Small Small
		♂ Holotype	Above { F. H.		Tr. 5, large 6 Faint pr. 1c, pr. 2, small pr. 3, small 4-5		
			Below { F. H.		Large 6 Tr. 1c, large pr. 2, pr. 3, 4, min. 5	Minute 3-4 Minute 2-5, 6	Minute Small
		♀ Unknown					
		♀ Holotype	Above { F. Prs. 2-3, irregular 4-6 H. Pr. 1b to S., prs. 1c-5, 6		Minute 2, 3-8, tr. 9 Pr. 1b to A., prs. 1c-3, 4-6	Tr. 10	
			Below { F. 1b, prs. 2-6, 7 H. Pr. 1b to S., prs. 1c-5, 6		2-8, tr. 9 Pr. 1b to A., prs. 1c-3, 4-6	Small 3-4 : small 10 Small 2-6	Minute Small
40	<i>monilijera</i>	♂ Allotype (from figure by Waterhouse & Lyell)	Above { F. H.		Small 1c, small prs. 2-3		
			Below { F. H. Trs. 3-4		Small 6-8 Small 1c-2, small pr. 3	Small 3-4 Small 3-6	Small Small
		Type not available					
		♂ Max.	Above { F. Prs. 1b-7 H. 1b to S., prs. 1c-7		Minute 1b-2, 3-9 F.prs. 1b-3, 4-6	10-11	
41	<i>eichhorni</i>		Below { F. Prs. 1b-7 H. 1b to S., prs. 1c-6, 7		Tr. 1b, 2-9 Streak 1a, f.prs. 1b-3, 4-7	Tr. 2, 3-6 : 9-11 Streak 1b, 1c-7	+ +
		♂ Min.	Above { F. Prs. 1b-3 : trs. 5-6 H. Prs. 1c-5, 6		Tr. 3 : small 5-8 F.prs. 1b-3, 4-5		
			Below { F. Prs. 1b-6 H. 1b, prs. 1c-5, 6		Minute 3, tr. 4, 5-8 F.prs. 1b-3, 4-5	Minute 4-5 : tr. 9, 10 4-7	Trace Minute F

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
42	lacon	♀ Max.	Above	F.	Prs. 1b-7	Minute 1b, 2-9	10-11	
				H.	1b to S., prs. 1c-6, linear 7	F.prs. 1b-3, 4-7		
		Below	F.	Prs. 1b-7.	Minute 1b, sending tongue between ads., 2-9	3-6 : 9-11	+	
			H.	1b to S., prs. 1c-6, 7	Streak 1a, f.prs. 1b-3, 4-7	1c-7	+	
		♀ Min.	Above	F.	Prs. 1b-7	Minute 2, 3-9	Small 10-11	
				H.	1b to S., prs. 1c-6	F.prs. 1b-3, 4-6		
		Below	F.	Prs. 1b-7	Minute 2, 3-9	Minute 3, 4-6 : 9-11	+	
			H.	1b to S., prs. 1c-6	Streak 1a, f.prs. 1b-3, 4-7	1c-7	+	
		♂ Holotype	Above	F.		Minute 3 : small 6-7		
				H.		Minute 5-6		
		Below	F.	Minute prs. 2-3	Minute 2-3 : 6-7	Streak 1b, large 2, 3, min. 4, 5-6	+	
			H.	Minute prs. 1c-4, 5-6	Minute 4, 5-6	Minute 1c-6	+	
		♂ Max.	Above	F.		2-3 : 6, small 7		
				H.		Minute 3, 4-6		
		Below	F.	Minute 2-3 on R. only	Minute 2-5, 6, min. 7-8	Streak 1b, 2-6	+	
			H.	Prs. 1c-5, 6	4-6, min. 7	1c-7	+	
		♂ Min.	Above	F.		Minute 6-7		
				H.				
		Below	F.		Minute 4-5, 6-7	Streak 1b, 2-3 : 6	+	
			H.		5-6	Minute 1c-6	Small	
♀ Allotype	Above	F.		Minute 3 : small 6-7				
		H.		4-6				
Below	F.		Minute 2-3 : 6-7, tr. 8	1b, large 2, 3 : tr. 5, 6	Small			
	H.	Prs. 2-4, 5 on R. only	4-6	1c-7	+			
Another ♀	Above	F.		Tr. 4 : 6-7				
		H.		4-6				
Below	F.		Minute 2, 3 : min. 5, 6-8	Double streak 1b, 2-6	+			
	H.	Minute 1b and pr. 1c, prs. 2-5	4-6	1c-7	+			
43	corinna	Type not available.						
	♂ Max.	Above	F.	Prs. 1b-7	Pr. 1b, 2-3, min. 4, 5-9, tr. 10	Faint 4-6 : 9-11		
			H.	1b to S., prs. 1c-6, 7	F. prs. 1b-3, 4-7			
	Below	F.	Prs. 1b-7	1b-9	2-6 : 9-11	Large		
		H.	1b to S., prs. 1c-6, 7	F. prs. 1b-3, 4-7	1c-7	+ with accessory		
	♂ Min.	Above	F.	Prs. 1b-3	1b-3 : 5-9	Small 10		
			H.	1b, faint prs. 1c-6	Prs. 1b-3, 4-6			

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
44	<i>rennelliensis</i> (Pl. 5, fig. 2)	♀ Max.	Below	F. Prs. 1b-3 irregular : prs. 5-6	1b-3 : 5-9	10	+
				H. 1b, prs. 1c-6	Prs. 1b-3, 4-6	Small 2-7	Small
			Above	F. Prs. 1b-7	1b-9, tr. 10	3-6 : 9-11	+
				H. 1b, prs. 1c-6, 7	Pr. 1b, f. prs. 1c-3, 4-7		
		♀ Min.	Below	F. Prs. 1b-7	1b-9	2-6 : 9-11, min. str. 12	+
				H. Prs. 1b-7	1a, streak at base 1b, pr. 1b, f. prs. 1c-4, 5-7	Pr. 1c, 2-8	+ with accessory
			Above	F. Tr. 3	1b-3 : 5-9	10	
				H. Faint prs. 3-6	Prs. 1b-3, 4-6		
		♂ Holotype	Below	F. Prs. 1b-3 : 5-6	1b-3 : 5-9	4-5 : 10	+
				H. 1b, prs. 1c-6	Prs. 1b-3, 4-6	2 : very small 4-7	Minute
			Above	F.	2-9		
				H. Fused prs. 1b-5 to S., 6	Fused prs. 1b-5 to A., small 6		
45	<i>umboina</i>	♂ Max.	Below	F.	2-9	Short streak 2	
				H. Fused prs. 1b-5 to S., 6	Fused prs. 1b-5 to A., 6		
			Above	F.	2-9		
				H. Fused prs. 1b-5 to S., 6	Fused prs. 1b-5 to A., small 6		
		♂ Min.	Below	F. 2-4	2-9	Streak 2, small 3, tr. 4	Trace
				H. Fused prs. 1b-5 to S., 6	Fused prs. 1b-5 to A., small 6	Tr. 2 : 4-5, tr. 6	Trace
			Above	F.	2-9		
				H. Fused prs. 1b-5 to S., 6	Fused prs. 1b-5 to A., small 6		
		♀ Unknown	Below	F.	2-9	2	
				H. Fused prs. 1b-4 to S., 5 postr. only to S., 6 postr. only	Fused prs. 1b-4 to A., small 5 to A.		
			Above	F.	6-7	6-7	
				H.	5-6		
46	<i>subnobilis</i>	♀ Holotype	Below	F.	Large 6-7, min. 8	2-6	Large
				H. Trs. prs. 2-4	5-6	Large 1c-7	+
		♂ Unknown	Above	F.	Small 6-7	Faint 3	+
				H.	Faint 4-6		
			Below	F.	4-7, min. 8	2-4 : 6	+
				H. Pr. 5, 6	4-6	1c-6	+
		♂ Max.	Above	F.	4-8	Faint 3-4	+
				H.	Faint 4-6		
			Below	F.	3-8	2-4 : 6	+
				H. Prs. 4-5, 6	4-6	1c-6	Large

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♂ Min.	Above { F. H.		Small 6-7	Faint 3	Faint
			Below { F. H.	Pr. 5, 6	4-7, min. 8 4-6	2-4 : 6 1c-6	+ Large
		♀ Ne-allotype (unique)	Above { F. H.		Trs. 5-7	1b : 3, tr. 4 : tr. 6	Large
			Below { F. H.	Prs. 4-5, 6	Tr. 3, small 4-8 4-6	2-4 : 6 Streak 1c, 2-7, an extra spot at base of 7	Trace Large
47	<i>illudens</i>	♂ Holotype	Above { F. H.		3-7 (5-6 largest)		
			Below { F. H.	Prs. 4-5, 6	3-8 (6-7 largest) 4-6	2-4 : min. 6 1c-7	Small +
		♂ Max.	Above { F. H.		Tr. 2, 3-7 4-6		
			Below { F. H.	Prs. 2-6, 7	2-8 2, pr. 3, 4-7	2-4, streaks 5-6 1c-6, tr. 7	+ Large
		♂ Min.	Above—F. H.				
			Below { F. H.		Minute 4-5, small 6-7 Minute 4, 5-6	2-3, tr. 4 2, min. 3-5, 6	Small Minute
		♀ Allotype	Above { F. H.		3-7 5-6		
			Below { F. H.	Prs. 4-5, 6	3-7, min. 8 Minute 3, 4-6	Large 2-4 Minute 1b, 1c-7	Large Large
		♀ Max.	Above { F. H.	3 Faint prs. 3-6	1b-8 Prs. 2-3, 4-7	3 3	
			Below { F. H.	1b, min. prs. 2-6, 7 Minute 1b, prs. 1c-6	Pr. 1b, 2-8 Prs. 2-3, 4-7 with an accessory 4 placed more proxi- mally	1b, large 2, 3-6 : min. 10 1c-7	Large with accessory +
		♀ Min.	Above { F. H.		6-7		
			Below { F. H.	Pr. 5, 6	3-6 4-6	2-4 1c-6	+ +
48	<i>mathiasana</i>	♂ Holotype	Above { F. H.		3-7 Small 6		
			Below { F. H.	6 (tr. pr. 5 on R. only)	3-8 Minute 3, 4-6	Small 2-4 1c-3, min. 4-5, 6	Small +
		♂ Max.	Above { F. H.		3-8 4-6		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
			Below { F.		Minute 2, 3-8	2-4	+
			H.	Prs. 4-5, 6	2, pr. 3, 4-6, min. 7	1c-6, min. 7	+
	♂ Min.		Above { F.		3-4, min. 5, 6-7		
			H.		Tr. 6		
			Below { F.		3-8	2-4	+
			H.	Tr. 5	4-6	2-6	+
	♀ Allotype not designated						
	♀ Max.		Above { F.		Tr. 1b, 2-8	1b, faint 2, 3-4 : faint 6	+
			H.		4-6	2-3 : 6	+
			Below { F.		1b-8	Streak 1b, 2-4 : 6	+
			H.	Prs. 4-5, 6	3-7	1c-7	+
	♀ Min.		Above { F.		2-6		
			H.		Faint 4, 5-6		
			Below { F.		2-6		+
			H.		4-6	2-3, min. 4-5, 6	+
49	<i>amycus</i> (from figures by Waterhouse & Lyell)	♂ fig. 18	Above { F.		3 : 5-8		
			H.		5		
			Below { F.		3 : 5-8	Minute 4	
			H.		4-6	2-6	Small
		♂ fig. 20	Above { F.		3-9		
			H.		4-5		
			Below { F.		4-8, tr. 9	2-3	
			H.			2-4, tr. 5	Small
	♀ not figured						
50	<i>reginae</i> (Pl. 9, fig. 5)	♂ Holotype	Above { F.	Prs. 1b-3, 4 (R only) small pr. 5, 6	Pr. 1b, 2-3 : 5-10	Tr. 4 : 9-11, min. 12	
			H.	1b to S., prs. 1c-6, 7	Prs. 1b-3, 4-6		
			Below { F.	Prs. 1b-7 (4 min.)	Pr. 1b, 2-3 : 5-9	2-6 : 8-11	Large
			H.	1b to S., prs. 1c-6, 7	Prs. 1b-3, 4-7	1c-7	+
		♂ Paratype	Above { F.	Prs. 1b-3, tr. pr. 4, prs. 5-6	Pr. 1b, 2-3, tr. 4, 5-9	10, tr. 11	
			H.	1b to S., prs. 1c-6, linear 7	Prs. 1b-1c, f. prs. 2-3, 4-7		
			Below { F.	Prs. 1b-6, 7	Pr. 1b, 2-3, tr. 4, 5-9	2-6 : tr. 9	+ with accessory
			H.	1b to S., prs. 1c-6, linear 7	Prs. 1b-1c, f. prs. 2-3, 1c-8 4-7		+
		♀ Allotype	Above { F.	Large prs. 1b-3, trs. prs. 4-5, tr. 6	1b-3, min. 4, 5-9	Minute 3, 4-5, min. 6, 10-11	Trace
			H.	1b, prs. 1c-6	Prs. 1b-3, 4-7		
			Below { F.	Large prs. 1b-6, 7	1b with accessory, 2-9	2-6 : 9-10, tr. 11	Large
			H.	1b, prs. 1c-6, lin- ear 7	Prs. 1b-3, 4-7	1c-7	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
51	<i>irene</i>	♂ Holotype	Above—F. H.				
			Below { F. H.			Elongated 2, 3, min. 4 : min. 9-10 2-6, linear 7	+ +
		♂ Max.	Above—F. H.				
			Below { F. H.			2-4 : min 9, 10 1c-7	Double Linear with accessory
		♂ Min.	Above—F. H.				
			Below { F. H.			2-4 4-6	+ +
		♀ Allotype	Above { F. H.			Faint 4-6	
			Below { F. H.			2-4 Tr. 2, small 3-4, 5-6	+ +
		♀ Max.	Above { F. H.			Faint 3 Faint 4-6	
			Below { F. H.			2-4 1c-7	+ +
		♀ Min.	Above—F. H.				
			Below { F. H.			2-4 Minute 2-3, 4-6	+ +
52	<i>eleutho</i>	♂ Holotype	Above { F. H.	Tr. pr. 3, prs. 4-6	1b-3 : 5-6, tr. 7, 8, tr. 9 F. prs. 1b-3, 4-6		
			Below { F. H.	Minute prs. 2-3 Minute pr. 1c : 3, prs. 4-6	1b-3 : 5-6, tr. 7, 8, 4-6 : 9-11 tr. 9 Small pr. 1b, f. prs. Trs. 4-5 1c-3, 4-6		Trace
		♂ Max.	Above { F. H.	Pr. 1b to S., prs. 2-3 : small prs. 5-6 1b, prs. 1c-6, 7	1b-3 : 5-9, tr. 10 1b, f. prs. 1c-3, 4-6	10-11	
			Below { F. H.	Pr. 1b to S., prs. 2-3, min. 4, prs. 5-6 Pr. 1b to S., prs. 1c-6	1b-3 : 5-9 1b, f. prs. 1c-3, 4-6	4-6 : 9-11 Small 1c : 4-6	Small Small
		♂ Min.	Above { F. H.	Prs. 4-5, 6	1b-3 : 5-6 : 8 F. prs. 1c-3, 4-6	Tr. 10	
			Below { F. H.	Minute pr. 2, 3 1b, pr. 1c : 3, prs. 4-5, 6	5-6, min. 7-8 F. prs. 1c-3, 4-6	4-6 : 9-11	
		♀ Allotype not designated					
		♀ Max.	Above { F. H.	Pr. 1b to S., prs. 2-3 1b, prs. 1c-6	1b-3 : 5-9 1b, f. prs. 1c-3, 4-6, tr. 7	Tr. 9, large 10-11	
			Below { F. H.	Pr. 1b to S., prs. 2-3 : 5, tr. 6 Pr. 1b to S., prs. 1c-6	1b-3 : 5-9 1b, f. prs. 1c-3, 4-7	4-6 : 8-11 1c : small 4-6	+ Small

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
53	<i>abjecta</i>	♀ Min.	Above	F. Trs. 2-3	5-6, min. 7, 8	10-11	
				H. Prs. 3-5, tr. 6	F.prs. 1c-3, 4-6		
			Below	F. Pr. 1b to S., prs. 2-3	5-6, min. 7, 8	4-6 : 9-11	Minute
				H. Minute prs. 1c-3, prs. 4-5	Pr. 1b, f.prs. 1c-3, 4-6	Minute 5	Trace
		♂ Holotype	Above	F.	2-3 : 5-6		
				H.	Prs. 2-3		
			Below	F.	2-3 : 6		
				H. Trs. 2-3	Prs. 2-3, tr. 4		
		♂ Max.	Above	F. Small pr. 2, 3	2-3, small 4, 5-6, min. 7-8	Tr. 10	
				H. Prs. 2-3, tr.pr. 4	Prs. 2-3, small pr. 4, tr. 5		
			Below	F. Prs. 2-3	Minute 1b, 2-3 : 5-6, min. 7-8	Minute strk. 4 : 10	
				H. 1c, prs. 2-3 to S., pr. 4	Small 1c, prs. 2-3 to A., small 4	Minute strks. 3-6	Trace
		♂ Min.	Above	F.	Tr. 2, 3 : 5-6		
				H.	Tr.pr. 3		
			Below	F.	2-3 : 5-6		
				H.	Small pr. 2, pr. 3		
		♀ Allotype	Above	F.	Tr. 1b, 2-3 : 5-6 : small 8	Tr. 10	
				H. Prs. 2-3 (3 to S.), 4	Prs. 2-3 (3 to A.), small pr. 4		
			Below	F. 2, pr. 3	1b-3 : 5-6, min. 7-8	Trs. strks. 4-5 : small 10	
				H. Minute 1c to S., prs. 2-3 to S., 4	1c to A., prs. 2-3, small pr. 4	Narrow 6, tr. narrow 7	
♀ Max.	Above	F. Ft.prs. 2-3	2-3 : 5-6 : 8	10			
		H. Prs. 2-3, tr. 4	Prs. 2-3, small pr. 4				
	Below	F. Prs. 2-3	Minute 1b, 2-3, small 5-6, trs. 7-8	Strk. 2, narrow strks. 4-5 : 10	+		
		H. Prs. 2-3 to S.	Prs. 2-3 to A., small pr. 4	Minute 3-4, narrow strks. 6-7	Minute		
♀ Min.	Above	F.	Short 2-3 : very small 5-6				
		H.	Short prs. 2-3				
	Below	F.	Minute 1b, 2-3 : 5-6				
		H. Tr.pr. 3	Short prs. 2-3				
54	<i>helcita</i>	♂ Holotype	Above	F.	3 : 5-6 : 8		
				H. Prs. 3-6, linear 7	Small 4-7		
			Below	F. Prs. 2-3 : 5-6, 7	2-3 : 5-6 : 8, tr. 9	3-6 : 10-11	+
				H. 1b, prs. 1c-6, 7	1c, prs. 2-3, 4-7	1c-7	+
		♂ Max.	Above	F.	2-3 : 5-6, min. 7, 8, min. 9	10-11	
				H. Prs. 2-6	Prs. 2-3, 4-7		
			Below	F. 1a, prs. 2-3 : 5-6	2-3 : 5-9	2-5, min. 6 : 10-11	+
				H. Prs. 1b-6, 7	1b, prs. 1c-4, 5-7	Pr. strks. 1c, 2-7 large	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
55	<i>aglaina</i>	♂ Min.	Above { F. H.		3 : 5-6 4-6		
			Below { F. H.	Small prs. 1c-5, 6	2-3 : 5-6 : 8 Minute prs. 2-3, 4-7	4 : 10 Small 1c-7	Minute Small
		♀ Allotype not designated					
		♀ Max.	Above { F. H.	Prs. 1c-6	2-3 : 5-8 Prs. 2-3, 4-7	10	
			Below { F. H.	Prs. 2-3 1b, prs. 1c-6, linear 7	2-3 : 5-9 Prs. 1c-3, 4-7	2-5, min. 6 : 10-11 1c-7	+ +
		♀ Min.	Above { F. H.	Prs. 4-6	3 : 5-6 : 8 Minute 3, 4-6	Tr. 10	
			Below { F. H.	Prs. 1b-6	Minute 2, 3 : 5-6 : 8 Trs. prs. 2-3, 4-7	1c-7	+
		♀ Holotype	Above { F. H.	Small prs. 3-6	Small 2-3 : 5-6 : 8 Ft. pr. 3, 4-6, all small	Small 10	
			Below { F. H.	1b, prs. 2-3 : trs. 6-7 1b, prs. 1c-6	2-3 : 5-6 : 8-9 1c, prs. 2-3, split 4, 1c-7 5-7	10-11	+ +
		♂ Of "maréensis"	Above { F. H.	Small pr. 3, prs. 4-6	2-3 : 5-6 : 8 4-6, tr. 7	10	
			Below { F. H.	1b, pr. 2, 3 : 5, pr. 6 Prs. 1c-6	2-3 : 5-6, min. 7, 8 Small 2, pr. 3, split 4, 1c-7 5-7	3-5 : 10, faint 11	Doubled +
		♀ Of "maréensis"	Above { F. H.	Faint prs. 2-4, 5-6	2-3 : 5-6 : faint 8 4-7	10	
			Below { F. H.	Faint pr. 2, 3 : 5-6 1c, prs. 2-6	2-3 : 5-6 : 8 1c and pr. 2 (on L 1c-7 only) 3-7	3-5 : 10-11	Doubled +
		Types not available					
56	<i>schmeltzi</i>	♂ Max.	Above { F. H.	Trs. 2-3 Tr. 1c, prs. 2-5, 6	2, pr. 3, 4-10, tr. 11 Prs. 1c-3, 4-6	Small 10-11	
			Below { F. H.	Prs. 2-6, 7 Prs. 1b-6, 7	2, pr. 3, 4-10, tr. 11 Prs. 1c-3, 4-6	3-6 : 9-11 Large 1c-7	Small +
		♂ Min.	Above { F. H.		6-9		
			Below—F. H.				
		♀ Max.	Above { F. H.	Prs. 1b-3 : 5-6 Prs. 1c-6	2-11 Prs. 1c-3, 4-6	10-11	
			Below { F. H.	Prs. 1b-3 : 5-6, 7 1b, prs. 1c-6	2-10 Prs. 1c-3, 4-6, tr. 7	3-6 : 9-11 Strk. 1c, 2-7	+ Large with accessory

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
57	<i>nechos</i> (Pl. 6, figs. 2, 6)	♀ Min.	Above { F. H.		5-9		
			Below { F. H.		5-9	10	
						Minute 6	Minute
		♂ Holotype	Above—F. H.				
			Below { F. H.			2-4 : 6	+
						2-6	+
		♂ Max.	Above—F. H.				
			Below { F. H.	Prs. 2-3 : 5 (on L. only) 4, pr. 5, 6	2-8 2, pr. 3, 4-6	2-6 : trs. 9-10 1c-7	+
		♂ Min.	Above—F. H.				
			Below { F. H.			3-4 2-6	+
		♀ Allotype not designated					
		♀ Max.	Above { F. H.			2-4 : 10 3	+
			Below { F. H.	Irregular 2-6 1c, prs. 2-6, 7	2-8 Prs. 2-4, 5-7	1b-6 : 9-10 1c-7	+
		♀ Min.	Above { F. H.			Tr. 3	Trace
			Below { F. H.	Prs. 4-5, 6	Minute 6 4-6	2-4 : 10 1c-7	+
58	<i>prusias</i> (Pl. 8, figs. 2-6)	♂ Holotype	Above—F. H.				
			Below { F. H.			2-4 1c-6	+
		♂ Max.	Above—F. H.				
			Below { F. H.			2-4 1c-7	+
		♂ Min.	Above—F. H.				
			Below { F. H.			Minute 3 3-6	+
		♀ Ne-allotype	Above { F. H.				Trace
			Below { F. H.			6 shows through 2-5 2-6	+
							with small accessory
		♀ Max.	Above—F. H.				
			Below { F. H.			2-5 2-6	+
							+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above—F. H.				
			Below { F. H.			2-4 4-6	+ +
59	<i>pronax</i> (Pl. 7, figs. 2, 6)	♂ Holotype	Above—F. H.			2-4, min. 5-6	+
			Below { F. H.			2-7	+
		♂ Max.	Above—F. H.			2-4, min. 5, 6	+
			Below { F. H.			1c-7	+
		♂ Min.	Above—F. H.			2-4	+
			Below { F. H.			2-6	+
		♀ Allotype	Above—F. H.			2-4	+
			Below { F. H.			1c-7	Large
60	<i>fraudulenta</i> (Pl. 2, fig. 5; Pl. 6, figs. 3, 7; Pl. 9, fig. 6)	♂ Holotype	Above—F. H.		Small 6	2-4 : small 10	Large
			Below { F. H. Prs. 4-6		Small 4-6	1c-7	Large
		♂ Max.	Above { F. H.		Trs. 3-6		
			Below { F. Prs. 2-7 H. 1c, prs. 2-6, linear 7		Pr. 2, 3-8 Minute 1c, prs. 2-3, 4-6, tr. 7	2-4, trs. 5-6 : tr. 9, 10 1c-7	+ +
		♂ Min.	Above—F. H.			Small 3-4	Small
			Below { F. H.			Small 2-6	Small
		♀ Allotype	Above { F. H.			Small 2-3	Small
			Below { F. H. Prs. 4-6		3-8 Pr. 4, 5-6	2-4 : min. 10 1c-7	Large Large
		♀ Max.	Above { F. H. Prs. 4-5, 6		Minute 3-8 Pr. 3, 4-6	1b-5 : 10 1c-7	+ Small
			Below { F. 1c, prs. 2-6, 7 H. Prs. 1c-6, 7		1b-8 1c, prs. 2-3, split 4, 5-7 ⁶	2-6 : 9-10. An accessory strk. on vein 4 Large pr. 1c, 2-7	+ + with accessory
		♀ Min.	Above { F. H.				Trace
			Below { F. H.			2-4 1c-6	+ Small

No.	Name	Example	Wings	Admarginals	Submarginals	Discais	Cell
61	<i>pyrgion</i> (Pl. 7, figs. 3, 7)	♂ Holotype	Above—F. H.				
			Below { F.		Minute 6-8	2-4	+
			{ H. Prs. 3-6		Pr. 3, 4-6	1c-6	+
		♂ Max.	Above—F. H.				
			Below { F. Minute 1b-3		Pr. 2 to D., 3-8	2 to S., 3-4 : 6 :	+
			{ H. 2, prs. 3-6, tr. 7		Pr. 3, 4-7	9-10 1c-7	Large with accessory
		♂ Min.	Above—F. H.				
			Below { F.			2-4	+
			{ H.			2-6	+
		♀ Allotype	Above { F.			Small 2-4	Small
			{ H.			6	
			Below { F. Prs. 2-5	2-8		2-4 : 10	+
			{ H.			1c-7	+
		♀ Max.	Above { F.			1b-3, tr. 4 : 10	+
			{ H.			1b	
			Below { F. 1b, prs. 2-6, 7	2-8		Strk. 2, 3-4 : min. 6 : 10	+
			{ H.	5-6		Pr. 1c, 2-6, min. 7	+
		♀ Min.	Above—F. H.				
			Below { F.			Oval 2, 3-4	+
			{ H.			Tr. 1c, 2-6, tr. 7	
62	<i>brenchleyi</i> (Pl. 8, figs. 3, 7)	♂ Holotype	Above—F. H.				
			Below { F.			2-3, min. 4	Small
			{ H.			2-6	+
		♂ Max.	Above—F. H.				
			Below { F.			2-4	Small
			{ H.			1c-7	+
		♂ Min.	Above—F. H.				
			Below { F.			Minute 2, tr. 3	
			{ H.			Small 3-6	Small
		♀ Allotype	Above—F. H.				
			Below { F.			2-3, min. 4	+
			{ H.			2-6	+
		♀ Max.	Above—F. H.				
			Below { F.			2-4	+
			{ H.			1c-7	+
		♀ Min.	Above—F. H.				
			Below { F.			Small 2-3	Small
			{ H.			3-6	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
63	<i>albomarginata</i> (Pl. 8, fig. 5)	♂ Allotype	Above—F. H.				
			Below { F. H.			Small 2-3 Small 2-6	Small Small
		♀ Holotype and paratype	Above—F. H.				
			Below { F. H.			Minute 2-3 3-6	Minute +
64	<i>era</i>	Type not available					
		♂ Max.	Above—F. H.				
			Below { F. H.	Prs. 4-5	5-6	2-4 1c-6	+ +
		♂ Min.	Above—F. H.				
			Below { F. H.			2-3 3-6	+ +
		♀ None seen					
65	<i>lapeyrousei</i> (Pl. 4, figs. 2, 6)	♂ Ne-allotype	Above—F. H.				
			Below { F. H.			2-4 Small 3-6	Small Small
		♂ Max.	Above—F. H.				
			Below { F. H.			Elongated 2, 3-4 1c-7	+ +
		♂ Min.	Above—F. H.				
			Below { F. H.			2-4 Small 3-6	Minute Small
		♀ Holotype	Above—F. H.				
			Below { F. H.			2-4 1c-6	Large Large
		♀ Max.	Above—F. H.				
			Below { F. H.	3, prs. 4-5, 6	Trs. 6-7	2-4 1c-7	+ +
		♀ Min.	Above—F. H.				
			Below { F. H.			2-4 1c-6	+ +
66	<i>matemae</i> (Pl. 4, figs. 3, 4)	♂ Holotype	Above—F. H.				
			Below { F. H.			2-4 1c-6	+ +
		♂ Max.	Above—F. H.				
			Below { F. H.	Minute 5-6		Elongated 2, 3-4 1c-6	+ +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
67	<i>torvina</i>	♂ Min.	Above—F. H.				
			Below { F. H.			2-4 1c-6	Trace +
		♀ Allotype and paratype	Above—F. H.				
			Below { F. H. Trace 5 in paratype			2-4 1c-6	+ +
		♂ Holotype	Above—F. H.				
			Below { F. H. Minute prs. 5-6			2 elongated, small 3-4 Small 1c-6	Small Small
		♂ Max.	Above—F. H.				
			Below { F. H. Prs. 3-6		Tr. 2, pr. 3, 4-6	2 (long curved bar), 3-4 1c-7	+ +
		♂ Min.	Above—F. H.				
			Below { F. H. Minute prs. 5-6			2-3 2-6	Small Small
		♀ Allotype	Above—F. H.				
			Below { F. H. Prs. 4-6			Elongated 2, 3-4 1c-6	+ +
		♀ Max.	Above—F. H.				
			Below { F. H. Prs. 3-6		Minute 4-6	2 elongated, 3-4 1c-7	+ +
		♀ Min.	Above—F. H.				
			Below { F. H. Prs. 4-6			2-4 1c-6	+ +
68	<i>bakeri</i>	♂ Holotype	Above—F. H.				
			Below { F. H.			2-4 2-6	+ +
		♂ Max.	Above—F. H.				
			Below { F. Pr. 6, 7 H. Prs. 4-6, 7		6	Elongated 2, 3-4 : small 6-7 1c-7	+ +
		♂ Min.	Above—F. H.				
			Below { F. H.			2-4 2-6	+ +
		♀ Allotype	Not designated.				
		♀ Max.	Above—F. H.				
			Below { F. H. Prs. 4-6			2-4 1c-7	+ +
		♀ Min.	Above—F. H.				
			Below { F. H.			2-4 Minute 1c-6	+ +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
69	<i>rileyi</i>	♂ Holotype	Above { F. H.	Faint prs. 4-6	5-8 Faint 5-6		
			Below { F. H.	Small prs. 2-3 : 5-6 1c, prs. 2-6	3-8 Split 4, 5-6	Elongated 2, 3-4 : 10-11 1c-7	Small +
		♂ Max.	Above { F. H.	Show through from beneath	Trs. 3-4, 5-8 5, the rest show through from beneath	10	
			Below { F. H.	1b, prs. 2-6, 7 1c, prs. 2-6, linear 7	2-8 1c, prs. 2-3, 4-7	Elongated 2, 3-4 : 10-12 1c-7	+ with accessory +
		♂ Min.	Above—F. H.				
			Below { F. H.			2-4 : tr. 10 2-6	Small +
		♀ Allotype	Above { F. H.		Trs. 2-5 on R, 2-3 on L, 6-8 2, pr. 3, 4-6	Tr. 10	
			Below { F. H.	Prs. 2-6 Prs. 3-6	2-8 2, pr. 3, 4-6	2-4 : 10-11 1c-7	Small +
		♀ Max.	Above { F. H.	Traces Prs. 3-6	2-8 1c, Prs. 2-3, 4-7	10	
			Below { F. H.	Prs. 1b-8 1b, prs. 1c-6, lin- ear 7	2-9 Prs. 1c-3, 4-7	2-4 : 10-11 1c-7	+ +
		♀ Min.	Above { F. H.			10	
			Below { F. H.		4 : 6-8	2-4 : 10-11 1c-7	+ +
70	<i>herrichii</i>	Type not available					
		♂ Max.	Above { F. H.	1b, prs. 2-3 2, prs. 3-6, 7	Pr. 1b, 2-10 Prs. 1c-3, 4-6	Tr. 10	
			Below { F. H.	Prs. 1b-6, 7 1b, prs. 1c-6	Pr. 1b, 2-10 1b, prs. 1c-3, split 4, 5-7	1b-6 : 9-11 1c-7	Split +
		♂ Min.	Above { F. H.		2-3 : 5-8 Faint 2, pr. 3, 4-6		
			Below { F. H.		2-3 : 5-8 Prs. 2-3, 4-6	Minute 3-4 Minute 4-6	Trace Small
		♀ Max.	Above { F. H.	Trs. 2-4 Prs. 3-6, 7	Pr. 1b, 2-10, tr. 11 Prs. 1c-3, 4-6, tr. 7	10-11	
			Below { F. H.	Prs. 1b-6, 7 1b, prs. 1c-6	1b-10 Prs. 1b-3, 4-7	2-5 : 9-11 1c-7	+ +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above { F. H. 2		1b-3, 5-9 Tr. pr. 1c, prs. 2-3, 4-6		
			Below { F. Tr. 3 H. Prs. 3-5, 6		1b-3, tr. 4, 5-8 Prs. 1c-3, 4-6	Tr. 2, 3-4 : 10-11 Trs. 2-3 : tr. 5	Trace +
71	<i>boisduvalii</i>	Type not available					
		♂ "A"	Above { F. H. Prs. 3-5, tr. 6		Trs. 2-3, small 4-8 Faint pr. 1c, small pr. 2, pr. 3, 4-6		
			Below { F. Prs. 2-3 : 5-6 H. Prs. 3-6		3-8, tr. 9 1c, pr. 2 : 4-6	Small 3-4 1c-7	Small Small
		♂ "B"	Above { F. H. Prs. 3-6		Minute 5-8 Tr. pr. 1c, prs. 2-3, 4-6		
			Below { F. Prs. 2-3 H. 1c, prs. 2-6		Small 2, 3, min. 4, 5-8, tr. 9 Small pr. 1c, prs. 2-3, 4-6	Minute 3-4 Small 3-6	Trace Small
		♀ None seen					
72	<i>mangoensis</i> (Pl. 2, fig. 6)	♂ Allotype not designated					
		♂ Max.	Above { F. H. Trs. 4-5		Small 2-7, tr. 8 Small 2, pr. 3, 4-6		
			Below { F. 2-3 H. Prs. 3-5, 6		Minute 2-8 1c, prs. 2-3, 4-6	2-5 : 10-11 Small 1c-7	++ Small
		♂ Min.	Above—F. H.				
			Below { F. H.			Minute 3-4 Minute 3-6	Trace Minute
		♀ Holotype	Above { F. H. Small, faint prs. 4-5		Small, faint, 1b-8 Faint 2, prs. 3-4, 5-6		
			Below { F. H. Prs. 4-5, 6 on L. only		2-8 2 : 4-6	3-4 1c-7	Minute +
		♀ Max.	Above { F. H. Prs. 3-5, 6		Small 1-3, 4-8 1c, prs. 2-3, 4-6		
			Below { F. H. Prs. 3-5, 6		Small 1b-8 Prs. 2-3, 4-6	2-4 : 6 : faint 10 1c-7	++ +
		♀ Min.	Above { F. H.		Minute 5-8 Tr. pr. 2, pr. 3, small 4-6		
			Below { F. H.		Minute 6-8 2, pr. 3, min. 4-6	Small 3-4 1c : 3-7	Trace +
73	<i>eurianassa</i>	On upper side completely fused and enlarged submarginals form a band on each wing with little indication of origin					
		♂ Holotype	Below { F. H.			Elongated 2, 3-4 2-6	++ +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♂ Max.	Above { F. H.			Small 3, tr. 4	
			Below { F. H.			Elongated 2, 3-4 : tr. 10 2-7	+ with accessory +
		♂ Min.	Below { F. H.			2-3	Trace
						4-6	+
		♀ Max.	Above { F. H.			Tr. 2, small 3	Small
			Below { F. H.			2-4 : tr. 10	+
						1c-7	+
		♀ Min.	Below { F. H.			2-3	+
						3-6	+
74	<i>inconspicua</i>	♂ Holotype	Above—F. H.				
			Below { F. H.			2-3	+
						2-6	+
		♂ Max.	Above { F. H.		Trs. 6-7		
			Below { F. H.			2-4 : 6 : 10	+
						1c-7	+
		♀ Allotype not designated					
		♀ Max.	Above { F. H. Traces		Faint 2-9 1b-2, pr. 3, 4-6		
			Below { F. Traces H. Prs. 4-5		2-9 Pr. 3, 4-6	2-4 : 6 1c-7	+
		♀ Min.	Above—F. H.				
			Below { F. H.			2-3 2-6	Minute +
75	<i>moesta</i>	♂ Holotype	Above { F. H.		Small 2-3 : 6-7		
			Below { F. H.			2 4	+
		♂ Max.	Above { F. H.	Minute pr. 3, 4	2-7		
			Below { F. H.			2-3 : 5-6 : 10 2-6	+
		♂ Min.	Above { F. H.		6, tr. 7		
			Below { F. H.			2	
		♀	None seen				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
76	<i>melander</i>	♂ Holotype	Above { F. H.		Trs. 2-3 : tr. 5, small 6-7		
			Below { F. H.		Small 6	2-6 : 10	+
		♂ Max.	Above { F. H.		2-3 : 5-7		
			Below { F. H.		Small 2-3 : 6	2-6 : 10 Pr. 1c, 2-6	+
		♂ Min.	Above { F. H.		Small 6-7		
			Below { F. H.			Small 2-3 Small 2-6	Small +
		♀ Allotype	Above { F. H.		Trs. 2-3 : tr. 5, small 6, tr. 7	Tr. 4, 5-6 : 9-10	+
			Below { F. H.			Large 2-6 : 9-10 Pr. 1c, large 2-7	Large Large
		♀ Max.	Above { F. H.		2-3 : 5-7	6 : min. 9, 10	
			Below { F. H.		Trs. 2-3 : faint 6	2-6 : 9-10 Pr. 1c, 2-7	Large Large
		♀ Min.	Above { F. H.		Minute 3 : small 6		
			Below { F. H.			2-6 : 10 Pr. 1c, 2-7	+
77	<i>magnipunctata</i> (Pl. 4, figs. 7, 8)	♂ Holotype	Above { F. Tr. 2 H.		2-3, min. 4, 5-7 Elongated prs. 1c-3, 4-6	6 : trs. 9-10 Small 7	
			Below { F. 1b, prs. 2-3, trs. 4-6 H. 1b, prs. 1c-5, 6		2-8 Tr. 1b, elongated prs. 1c-3, 4-6	2-6 : 9-10 Tr. 1b, pr. 1c, 2-7	+
		♂ Max.	Above { F. Tr. 2 H.		Tr. 1b, 2-7 Elongated prs. 1b-3, 4-6	6 : tr. 9, small 10	
			Below { F. 1b, prs. 2-3, 4, tr. 5, 6-7 H. 1b, prs. 1c-5, 6		2-8 Tr. 1b, elongated prs. 1c-3, 4-6	2-6 : 9-10 Tr. 1b, pr. 1c, 2-7	+
		♂ Min.	Above { F. H.		2-3, trs. 4-5, 6-7 Prs. 1c-3, 4-6		
			Below { F. H.		2-3, small 4-5, 6-7 Prs. 1c-3, 4-6	2-6 : 10 1c-7	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell		
78	<i>tristis</i> (Pl. 2, fig. 7)	♀ Allotype	Above	F.		Tr. 1b, 2-7, min. 8	4-6 : 9-10	Trace	
				H.		Prs. 1c-3, 4-6	Show through from below		
			Below	F.	1b, prs. 2-3, tr. 4	1b-8	1b-6 : 9-10	+	
				H.	1b, prs. 1c-5	Tr. 1b, prs. 1c-3, 4-6	Pr. 1c, 2-7	+	
		♀ Max.	Above	F.		Tr. 1b, 2-7, min. 8	4-6 : 9-10		
				H.		Prs. 1c-3, 4-6	7		
			Below	F.	1b, prs. 2-4	1b-8	1b-6 : 9-10	Large	
				H.	1b, prs. 1c-6	1b, prs. 1c-3, 4-6	Tr. 1b, pr. 1c, 2-7	Large	
		♀ Min.	Above	F.		2-7			
				H.		Prs. 1c-3, 4-6			
			Below	F.	Prs. 2-3	2-8	2-6 : 9-10	+	
				H.	Minute 1b, prs. 1c-6	Tr. 1b, prs. 1c-3, 4-6	1c, 2-7	+	
		♂ Holotype	Above	F.		2-3, min. 4-5, 6-7			
				H.		2, small pr. 3, 4-6			
			Below	F.	1b, prs. 2-3, 4	2-3, min. 4-5, 6-7	2-6 : tr. 10	+	
				H.	Irregular traces	Tr. 4, trs. 2-3 on L.	1c-6, and 7 on R.	+	
		♂ Max.	Above	F.	1b, prs. 2-3	1b-7	Tr. 6 : trs. 9-10		
				H.		Prs. 1b-3, 4-7	7		
			Below	F.	Prs. 1b-5, 6, min. 7	1b-7, min. 8 : 10	2-6 : tr. 9, 10	+	
				H.	1b, prs. 1c-5, 6	Prs. 1c-3, 4-6	Pr. 1c, 2-7	+	
		♂ Min.	Above	F.		6-7			
				H.		Minute 4, 5, min. 6			
			Below	F.		7	2-6 : 10	Small	
				H.		1c, prs. 2-3, 4	2 : 4-6	+	
		♀ Allotype not designated							
		♀ Max.	Above	F.	Tr. 1b, pr. 2, 3	Pr. 1b, 2-3, min. 4, 5-7	4-6, min. 7 : 9-10	Large	
				H.	Prs. 1c-4, 5	1b, prs. 1c-3, 4-6	3-6		
			Below	F.	Prs. 1b-4, 5	Pr. 1b, 2-8	2-6 : tr. 8, 9-10	Large	
				H.	1b, prs. 1c-6	1b, pr. 1c with streak between the members, prs. 2-3, 4-6	1c-7	+ with accessory	
		♀ Min.	Above	F.		2-3 : 5-7	10		
				H.		Prs. 1c-3, 4-6			
			Below	F.		5-7	2-6 : 10	+	
				H.		Prs. 1c-3, 4-5	1c-7	+	
79	<i>pelor</i>	Types not available							
♂ Max.	Above	F.		2-3, small 4-5, 6-8	5-6 : 9-10				
		H.	Small 1b, prs. 1c-5, 6	1b, f.prs. 1c-3, 4-6	7				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
			Below {	F. 1b, prs. 2-6, 7	Small 1b, 2-8	1b-6 : 9-11	+
				H. 1b, prs. 1c-6	Large 1b with basal streak, prs. 1c-3, 4-7	1c-7	+
♂ Min.			Above {	F.	2-3, min. 4-5, 6-7	6 : 10	
				H.	1b, f.pr. 2, pr. 3, 4-6		
			Below {	F. Prs. 2-5	2-8	Minute 2-4, 5-6 : 10	Small
				H. Small 1b, prs. 1c-5, 6	1b, prs. 1c-3, 4-6	2-6	+
♀ Max. (= <i>sylvester</i>)			Above {	F. Prs. 1b-3	1b-8	4-6 : 9-11	Trace
				H. F.pr. 1b, prs. 1c-5	1b, f.prs. 1c-6		
			Below {	F. Prs. 1b-6, 7	1b-8	1b-6 : 9-12	+
				H. 1b, prs. 1c-6	1b, f.prs. 1c-6, 7	Pr. 1c to S., 2-7	+ with fused accessory
♀ Min.			Above {	F.	2-3, small 4-5, 6-7, tr. 8		
				H.	Small 1b, prs. 1c-3, 4-6		
			Below {	F. 1b, prs. 2-5, 6	2-8	1b-6 : 9-10	+
				H. Prs. 1b-5	Small 1b, prs. 1c-3, 4-6	1c-7	+
80 <i>sylvester</i>		Types not available					
♂ Max.			Above {	F. 1a and pr. 1b to S., prs. 2-3	1a and pr. 1b to A., 2-3, min. 4-5, large 6-7, tr. 8	5-6 : 9-10, tr. 11	
				H. 1b to S., prs. 1c-6, 7	Large prs. fused 1b-6		
			Below {	F. Prs. 1b-7	Pr. 1b, 2-8	2-6 : 9-12	+
				H. 1b to S., prs. 1c-6, 7	Large prs. fused 1b-6, 7	Pr. 1c, 2-7	+
♂ Min.			Above {	F.	Pr. 1b, 2-3 : 6-7	Tr. 6 : 10	
				H.	Prs. 1b-1c, f. prs. 2-3, 4-6		
			Below {	F. Prs. 1b-4	Pr. 1b, 2-3, min. 4-5, 6-7	Minute 2-4, 5-6, tr. 9, 10	
				H. 1b, prs. 2-5, 6	1b-6	1c-6	+
♀ Max.			Above {	F. Pr. 1b to S., prs. 2-3, trs. 4-5	1a, pr. 1b to A., 2-3, min. 4-5, 6-8	4-6 : 9-12	
				H. 1b to S., prs. 1c-5, 6	Large prs. fused 1b-6		
			Below {	F. 1a, pr. 1b to S., prs. 2-7	Pr. 1b to A., 2-8	Pr. 1b, 2-6 : 9-12	+
				H. 1b to S., prs. 1c-6, 7	1a-1b filled white, large prs. fused 1c-6, tr. 7	Pr. 1c, 2-7	+
♀ Min.			Above {	F.	1b-3 : 6-7	6 : 9-10	
				H.	Pr. 1c, large prs. fused 2-6		
			Below {	F. Irregular 1b-3	Pr. 1b, 2-3, min. 4-5, 6-8	Minute 2-4, 5-6 : 9-10	+
				H. 1b, prs. 1c-5	Large prs. fused 1b-6	1c-7	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
81	<i>dardanoides</i>	Types not available					
		♂ Max.	Above { F. H.		2-3, small 4-5, 6-7 Prs. 1c-3, 4-6	Small 6 : 9-10	
			Below { F. H.	Irregular traces	2-7, tr. 8 Trs. prs. 1c-3, 4-6	2-6, tr. 9, 10, tr. 11	+
		♂ Min.	Above { F. H.		2-3, min. 4-5, 6-7, Prs. 1c-3, 4-5, 6 obscured	Tr. 6 : 10	
			Below { F. H.		2-3, min. 4-5, 6-7 Prs. 1c-3, 4, 5 ob- scured	5-6 : 10, tr. 11	+
		♀ Max.	Above { F. H.		Large 2-3, min. 4-5, 6-7 Tr. pr. 1c, prs. 2-3, 4-6	5-6 : 9-10	
			Below { F. H.	Prs. 2-5, 6	2, large 3, min. 4-5, 6-7, min. 8 Tr. pr. 1c, prs. 2-3, trs. 4-6	1b-6 : 9-11 Minute 3-6	+ Small
		♀ Min.	Above { F. H.		Large 2-3, tr. 5, 6-7 Tr. 1c, prs. 2-3, 4-6	5-6 : 9-10	
			Below { F. H.		Large 2-3, min. 4-7 Tr. 1c, prs. 2-3, trs. 4-5	2-6 : 9-11	+
82	<i>treitschkei</i>	♂ Holotype	Above { F. H.		Minute 4-6	Streak 1b, small 3, tr. 4	Small
			Below { F. H.		Small 4-6	2-4 Small 1c-7	+ +
		♀ Ne-allotype	Above { F. H.		4-7	Double streak 1b : small 3-5, 6 Large 1c, 2-7	Small
			Below { F. H.		4-7	Streak 1b, 2, small 3-4 : small 6 Large 1c, 2-7	+ +
83	<i>eugenia</i>	♂ Allotype not designated					
		♂ Max.	Above { F. H.		5-6 4-6	3-4, tr. 5	+
			Below { F. H.		4-6	Small 2-4 1c-7	+
		♂ Min.	Above { F. H.		Trs. 5-6 5	Small 3-4	+
			Below { F. H.		4-6	Trs. 3-4 Minute 2-5	+ Minute
		♀ Holotype	Above { F. H.		Large 5-6 1c, pr. 2, pr. 3 to D3, large 4-6, 7 shows through from below	Streak 1b, 2-6 2-6	+ +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
84	<i>dampierensis</i>	♀ Max.	Below { F. H.		Small 4, large 5-6 2-6	Streak 1b, 2-6 : 9 1c-7	+ +
			Above { F. H.		5-6 1c, pr. 2 to D., 3, 4 to D., 5-7	1b-6 2 to S., 3, 4 to S., 5-7	+ Small
			Below { F. H.		Small 4, large 5-6 1c, pr. 2, pr. 3 to D3, large 4-6, 7 shows through from below	Streak 1b, 2-6 : 9 1c-7	+ doubled +
			Above { F. H.			2-4	+
		♀ Min.	Below { F. H.		2, tr. 3, 4-6	Small 2-4	+
			Above { F. H.			2-4	+
			Below { F. H.		4-6	2-6	+
			Above { F. H.		Large 5-6 4-5, clear white	Minute 3-4	Small
		♂ Max.	Below { F. H.		5-6 4-6	2-4 2-6, small 7	+ with accessory +
			Above { F. H.		3-4 : tr. 6 4-6		+
			Below { F. H.		5-6 4-6	2-4 1c-7	+
		♂ Min.	Above { F. H.				Small
			Below { F. H.			3 Minute 3-4	+
		♀ Max.	Above { F. H.		5-6 4-6	1b-4 2-4 : 6	+
			Below { F. H.		5-6 Small 2 : 4-6	2-4 1c-7	+
		♀ Min.	Above { F. H.			1b-4 2-5	+
			Below { F. H.		4-6	2-4 1c-6	+
		♂ Holotype	Above { F. H.		Small 5-6 Minute 4-5	Streak 1b : small 3	Small
			Below { F. H.		Minute 5, small 6 Small 4-6	2-4 Minute 2-6	+ with small accessory +
		♀ Allotype	Above { F. H.		Large 5-6 Small pr. 2, 4-6	Faint 1b : 5-6 2-6	Small +
			Below { F. H.		5-6 Small pr. 2, 4-6	2-4 : min. 6 2-6	+

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell		
86	<i>gaedei</i> (Pl. 3, fig. 1)	♂ Holotype	Above	{ F. H.	Small 4-5	Small 3	+		
			Below	{ F. H.	Minute 4-5	2-3, min. 4	+		
		♀ Allotype	Above	{ F. H.	5-6	2 shows through small 3-4	Very small		
			Below	{ F. H.	5-6	2-5, 6 shows through			
				{ F. H.	Narrow prs. 1c-2 : 4-6 rounded	Streak 1b, 2-4	+		
				{ F. H.	Narrow prs. 1c-2 : 4-6 rounded	2-6	Minute		
87	<i>caerulescens</i> (Pl. 3, fig. 5)	No types available							
88	<i>eulegnica</i>	♂ Holotype	Above	{ F. H.		Tr. 6	Small		
			Below	{ F. H.	Small 5-6	Small 2, min. 3 : tr. 6	+		
		♂ Max.	Above	{ F. H.	Small 5-6	Elongated 1c, tr. 2, 3-6	Small		
			Below	{ F. H.	Minute 1c : small 4-6	Small 2-4 : 6	+		
		♂ Min.	Above	F. H.	Minute 6	Large 2, 3-4 : 6	+ with accessory		
			Below		4-6, min. 7	1c-7	+		
		♀ Allotype	Above	{ F. H.	Small 5-6	2, tr. 3	+		
			Below	{ F. H.	Small 5-6	Minute 3-4 : 6	+		
				{ F. H.	Small 5-6	Faint Str. 1b, tr. 2, 3	+		
				{ F. H.	Small 5-6	Small 2-3	Trace		
		♀ Max.	Above	{ F. H.	4-6	Str. 1b, large 2, 3-4 : tr. 6 on L.	+		
			Below	{ F. H.	5-6	1c-6, tr. 7	+		
				{ F. H.	1c : large 4-7	3-4 : 6	+		
				{ F. H.	5-6	2-3 : 6	+		
		♀ Min.	Above	{ F. H.	4-7	Two stripes 1b, large 2, 3-4 : 6	Large		
			Below	{ F. H.	Tr. 3	1c-7	+		
				{ F. H.	5	3	Trace		
				{ F. H.	2-3	+			
		{ F. H.	5-6	1c-3 : 5-6	+				
		89	<i>viridis</i> (Pl. 3, fig. 4)	♂ Lectotype (<i>decia</i> Fr.)	Above	{ F. H.	2 : 4-5	Str. 1b : small 3	Small
					Below	{ F. H.	Minute 2 and 4-5	Tr. 3	
						{ F. H.		Minute 3-4	Minute 3 and 5-6

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Holotype	Above { F. H.		1c-6	1b (2-4 showing through)	
			Below { F. H.		1c, 2, small 3, 4-6	Str. 1b, small 2-4 Small 4-6	+ with accessory
90	<i>jessica</i> (Pl. 3, figs. 6, 7, 8)	♂ Holotype <i>jessica</i> Butler, 1869	Above { F. H.		United with discals	Large 1b, a patch in ant. corner of 2, a patch at base of 3 Pair 1c, 2-6	+
			Below { F. H.		United with discals, separate 5-6	2-4 : tr. 10 Pair 1c, 2-4, separate 5-6	+ with small accessory
		♂ Type of <i>lorenzo</i> Butler, 1870	Above { F. H.		United with discals, separate 5-6	1b : elongated 3 Pair 1c, 2-4, separate 5-6	
			Below { F. H.		United with discals, separate 4-6	Elongated 3, min. 4 Pair 1c, 2-3, separate min. 4, 5-6	Small Small
		♂ Type of <i>erimas</i> G. & S. 1878	Above { F. H.	Large whitish discal patch occupying middle of 1b, basal half 2 (except for a dark triangle), bases 3-6 : 10, and outer half of postr. part of cell.		1b, fused pr. 1c, 2-4 Separate 5-6	Large
			Below { F. H.			Str. 1b, large 2-6 : small 9-11 Elongated whitish patches in Subm. and Discal areas, pair 1c, 2-4 Separate 5-6	Very large Large
		♀ Ne-allotype <i>jessica</i>	Above { F. H.	Spots much enlarged forming a nearly complete dyslegnic discal patch occupying outer 2/3 cell and bases of areas mentioned, except that in 2 there is dark ground colour at extreme base		1b-6 : 9-10. Much enlarged	Fills outer two-thirds
			Below { F. H.	As on upper side. Proximal end of the outer spot in 1c, and 4, has captured the true Discal 1c and 4		1b-5, small 6 : small 9, 10 5-7	Fills half Fills half
		♀ Ne-allotype of <i>lorenzo</i>	Above { F. H.	Row of eulegmic creamy-white large spots (Subm. 1c-6). All except 5-6 forked distally. In 1c the members of the pair not completely fused		Faint dyslegnic streaks 1b-4 : spot 3 Minute D4 at central end of the large Sub. 4	Faint patch
			Below { F. H.	As on upper side, but paired origin shown at peripheral end more clearly		1b-4 4-6	Small, paired +

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Ne-allotype <i>erimas</i>	Above { F. Central white patch from vein 1 to area 11 and white streak along costa. Small residual dark triangular area base of area 2. 1a, base of 1b, and base of cell dark H. Subs. and Discals 1c-7 coalesced to form continuous white band. Spots 2-5 fill bases of areas : in 6-7 base is dark				Apical half white
			Below { F. 1a-6 and 9-11 more or less white. 1a-1b white as far as the broad dark border : black streak 1b close to vein 2 : in 2 at base a residual black arrowhead mark, apex outlined white : 3 white at base : in 4 extreme base dark, beyond this a rectangular white area : area 5 similar : 6, 9, 10 white at base : white spot in 11 in line with 10 : white streak in 12 H. Spots discrete. Streaks at bases 1a-1b. Two elongated discal patches 1c of which external is largest and joins Sub. 1c : in 2a horseshoe patch with D. joined to pair Subs : 3 small rectangular basal spot, 4D combined with sub. : 5 separate D. and Sub. : 6D just connects with Sub. : 7 pear shaped : spot at base of 9				Mostly white
91	<i>aenea</i> (Pl. 3, fig. 3)	♂ Holotype	Above { F. H.			1b, tr. 2, small 3-4	Small
			Below { F. H.			2	Large
		♀ Allotype	Above { F. H.			Streak 1b, 2-4 showing through, 5-6 : tr. 9, small 10	Trace
			Below { F. H.	2 : 4, tr. 5		2-6	+
						1c-3, 4-6 showing through	+
						2-6 : 9-10	Large
				4-5		1c-7	+
92	<i>suffusca</i>	♂ Holotype	Above { F. H.			Small 3	Small
			Below { F. H.			2-4	+
						Small 3-6	Small
		♂ Paratype A	Above { F. H.			Small 3, tr. 4	
			Below { F. H.			Small 2-4	+
				Small 4		Small 2-6	Minute
		♂ Paratype B	Above { F. H.			Minute 4	Trace
			Below { F. H.			Small 3-4	+
				Small 3, tr. 4		2	+
		♀ Allotype	Above { F. H.			Trs. 3-4	
			Below { F. H.			Small 3-6	
						Large 2-4, tr. 5	+
						Large 2-6, tr. 7	+
93	<i>asyllus</i> (Pl. 1, fig. 5, Pl. 6, figs. 4, 8)	♂ Holotype	Above { F. H.	3-8 5		1b : 3-6 : 9, large 10	
			Below { F. H.	Prs. 2-6, tr. 7 1b, prs. 2-6	2-8 Prs. 1c-3, 4-7	2-6 : 9-10 1c-7	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
	♂ Max.	Above	{ F.		2-8	1b, 2-6 : 9-10	
			{ H. 1b, prs. 1c-6		Prs. 1c-3, 4-7	1c-7	
		Below	{ F. Prs. 1b-6, 7		2-8	2-6 : tr. 9, 10	
			{ H. 1b, prs. 1c-6		Prs. 1c-3, 4-7	1c-7	
	♂ Min.	Above	{ F.				
			{ H.		6		
		Below	{ F.		4-8	2-6 : 10	
			{ H. 2, prs. 3-4		3-7	1c-7 (min. 1c, 4 and 6)	
	♀ Allotype	Above	{ F.		2-7	1b, min. 2, 3 : 5, min. 6 : 10	
			{ H.		5-6	3	
		Below	{ F. Prs. 2-4 : faint 6		Large 2-8	Large 2-6 : 10, tr. 11	
			{ H. Large 1c, prs. 2-6		Large prs. 1c-3, 4-7	Large 1c-7	
	♀ Max.	Above	{ F.		2-7, tr. 8	1b-6 : 9-10	
			{ H.		4-7	1c-4	
		Below	{ F. Prs. 1b-6, 7		1b-8	1b embedded in general whiteness, 2-6 : 10, tr. 11	
			{ H. 1b, prs. 1c-6		1b, prs. 1c-3, 4-7	Pr. 1c, 2-7	
	♀ Min.	Above	{ F.			10 (faint trace only)	
			{ H.		6		
		Below	{ F.		Small 4-8	2-6 : 10	
			{ H. Minute pr. 2, prs. 3-4		Prs. 2-3, 4-7	1c-7	
94	<i>gerion</i>	♂ Ne-allotype Above	{ F.				
			{ H.		Pr. 3, 4		
		Below	{ F.		Small 3-7, tr. 8	2-6 : 10	
			{ H.		5-7	1c-7	
	♀ Holotype	Above	{ F.			Trs. 5-6 : tr. 9, 10	
			{ H.		6		
95	<i>dudgeonis</i>	♂ Holotype Above	{ F.		Small 1b, 2-8, tr. 9		
			{ H.				
		Below	{ F.		Minute 4	2 large	
			{ H.		Minute 4-5, small 6-7		
	♂ Max.	Above	{ F.		Small 1b-9		
			{ H.		Small, blue, 4-6		
		Below	{ F. Minute 1b, prs. 2-6, 7		Minute 2 : min. 4	2 large	
			{ H. Pr. 2-3, 4		Tr. 3, small 4-7		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
96	<i>tulliolus</i>	♂ Min.	Above { F. H.		Small and faint 2-7 tr. 8		
			Below { F. H.		Minute 6	2	
		♀ Allotype	Above { F. H.		1b-9 pale and diffuse, tr. 10 4-6		
			Below { F. H.		2-9, more defined 4-7, well defined		
		♀ Max.	Above { F. H.		1b-9, tr. 10 4-6		
			Below { F. 1b, prs. 2-3, 4 H. Prs. 1c-4		1b-8 Ft. pr. 2, small pr. 3, 4-7	2 large	
		♀ Min.	Above { F. H.		Small, faint, 1b-5, 6-7, trs. 8-9		
			Below { F. H.		4-7	2	
		♂ Holotype (fig. in Jones' "Icones" Vol. 3, Pl. 67)	Above { F. H.		1b-9	10	
			Below { F. Prs. 1b-7 H. Prs. 1b-4, 5		Pr. 1b, 2-4, large 5-6, 7-9 Small prs. 2-3, 4-7	2 : 10	
		♂ Max.	Above { F. H.		1b-9 Trs. 2-5, 6	10	
			Below { F. Prs. 1b-7 H. 1b, prs. 1c-5		Pr. 1b, 2-9 Prs. 1c-3, 4-7	2 : 10 : 12	
		♂ Min.	Above { F. H.		1b-9	10	
			Below { F. Prs. 1b-2 : pr. 4, 5 H. 1b, prs. 1c-3, 4		1b-9 Tr. 3, 4-6	10	
		♀ Lectotype (<i>turneri</i> Butler, 1878)	Above { F. H.		1b-5, large 6, 7-9	10	
			Below { F. 1b, prs. 2-6, 7 H. 1a-1b, prs. 2-4		Pr. 1b, 2-9 Prs. 1c-3, 4-7	2 : 10	
		♀ Max.	Above { F. H. Traces 2-3		1b-9 (5-7 fused) tr. 10 Faint prs. 2-3, 4-6	10	
			Below { F. Prs. 1b-7 H. 1b, prs. 1c-5		Pr. 1b, 2-9 Prs. 1c-3, 4-7	2 : 10 : 12	
		♀ Min.	Above { F. H.		1b-9	10	
			Below { F. 1b, prs. 2-5 H. Prs. 2-4		1b-9 3-6	2 : 10	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
97	<i>goodenoughi</i>	♀ Holotype	Above—F. H. Below—F. H.	{ See p. 112 for description. The specimen was not seen on final revision, and the usual tabular statement cannot be given			
		♂ Unknown					
98	<i>forsteri</i> with <i>incompta</i>	♂ Holotype	Above { F. H.		Pr. 1b, 2-9		
			Below { F. Prs. 1b-6 H. 1b, prs. 1c-3, 4		Pr. 1b, 2-9 Small pr. 3, 4-7	Very small 10	
		♂ Max.	Above { F. H.		Pr. 1b, 2-9, tr. 10 4-5		
			Below { F. 1a, prs. 1b-7 H. 1a, 1b, prs. 1c-5		Pr. 1b, 2-9 1b, 1c, prs. 2-3, 4-7	2 : 10	
		♂ Min. (= <i>incompta</i>)	Above—F. H. Below—F. H.				
		♀ Type not designated					
		♀ Max.	Above { F. H.		1b-9, small 10 Trs. 4-6		
			Below { F. Prs. 1b-7 H. 1b, prs. 1c-5, tr. pr. 6		Pr. 1b, 2-10 Prs. 1c-3, 4-7	10	
		♀ Min. (= <i>incompta</i>)	Above—F. H. Below—F. H.				
99	<i>adyte</i>	♂ Holotype	Above { F. H.		Pr. 1b : very small 4-6, tr. 7 6-7		
			Below { F. Minute. Pr. 1b, 2 : 4 H. Prs. 1c-4, 5		Very small 4-6 : 8-10 Minute 2, small pr. 3, 4-7		
		♂ Max.	Above { F. H.		Pr. 1b, 2-9 Trs. 4-5, 6-7		
			Below { F. Faint 1b, 2 : 4-5 H. 1b, prs. 1c-4, 5		Pr. 1b, faint 2-3, 4-10 1b, faint pr. 1c, prs. 2-3, 4-7		
		♂ Min.	Above—F. H.				
			Below { F. H. 1c, prs. 2-4		Minute pr. 1b : 4-6 4-7		
		♀ Allotype not designated					
		♀ Max.	Above { F. H.		1b-9		
			Below { F. Prs. 1b-6, 7 H. 1b, prs. 1c-4, 5		Pr. 1b, 2-10 1b, prs. 1c-3, 4-7		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above { F. H.		4-6		
			Below { F. H.	Irregular traces	1b : 4-9 4-6		
100	<i>darchia</i>	♂ Type not available					
		♂ Max.	Above { F. Faint prs. 1b-2 H. 1c, prs. 2-6		Large 1b, 2-4, large 5-6, 7-10 Pr. 1c joined distal- ly, prs. 2-3 joined centrally, F. prs. 4-5, 6-7	7 : 10	
			Below { F. Prs. 1b-7 H. 1b, prs. 1c-5, 6		Large 1b, 2-4, large 5-6, 7-10 1b with streak, prs. 1c-3 not joined, 4-7	1b-2 : 6 : 10-12 2, tr. 3, 4-5 : linear 7	Elongate
		♂ Min.	Above { F. H.		Large 1b, 2-4, large 5-6, 7-10 Prs. 1c-3 not joined, 4-7	10	
			Below { F. Trs. 1b-3 H. Minute prs. 1c-4		Large 1b, 2-4, large 5-6, 7-10 Prs. 1c-3 not joined, 4-6	2-10	
		♀ Type not available					
		♀ Max.	Above { F. Small prs. 1b-2 H. Prs. 1c-4		Large 1b, 2-4, large 5-6, 7-10, Tr. 11 Prs. 1c-3 not joined, 4-7	7 : 10	
			Below { F. Prs. 1b-7 H. 1b, prs. 1c-6		Large 1b, 2-4, large 5-6, 7-10 Prs. 1c-3 not joined, 4-7	1b-3 : 6 : 10-12 2-3 : 5 : 7-8	Trace
		♀ Min.	Above { F. H. Trs. prs. 1c-4		Large 1b, 2-4, large 5-6, 7-10 Prs. 1c-3 not joined, 4-7	10	
			Below { F. Prs. 1b-6 H. 1b, prs. 1c-4		Large 1b, 2-4, large 5-6, 7-10 Prs. 1c-3 not joined, 4-7	2 : 10	
101	<i>niveata</i> (Pl. 9, fig. 7)	♂ Holotype	Above { F. H.		1b-5, large 6, 7-8 Series of marginal patches 1b-4, smaller patch 5, round spot 6	10	
			Below { F. Prs. 1b-6, 7 H. Pair 5		1b-5, large 6, 7-9 Series of marginal patches 1b-4, smaller patch 5, spots 6-7	Elongate 2 : 10	
		♂ Max.	Above { F. Trs. 1b-2 H.		1b-9, tr. 10 Marginal patches 1b-6, spot in patch in 6, spot 7	10	
			Below { F. Prs. 1b-7 H. Prs. 5-6		Pr. 1b, 2-9 Marginal patches 1b-6 (5 and 6 shorter), spots 6-7	2 : 10 : 12 7 (dyslegnic)	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell		
102	<i>pyres</i>	♂ Min.	Above	F.		1b-8	10		
				H.		Spot 1b, larger patches 1c-4, spots 5-6			
			Below	F.	Prs. 1b-6, 7	1b : 9	2 : 10		
				H.	Pair 5	Marginal patches 1b-4, smaller patch 5, spots 6-7			
		♀ Type not designated							
		♀ Max.	Above	F.	Trs. 1b-2	1b-9	10		
				H.	Pair 6	Marginal patches 1b-5, spot 6			
			Below	F.	Prs. 1b-7	1b-9	2 : 10 : 12		
				H.	1b, prs. 1c-6	Marginal patches 1b-4, smaller 5, spots 6-7	7 (dyslegnic)		
		♀ Min.	Above	F.		1b-9	10		
				H.	Pr. 5, 6	Patches 1b-4, 5 smaller, 6 spot	10		
			Below	F.	Prs. 1b-6	1b-9	2 : 10		
				H.	Pr. 5, 6	Patches 1b-4, 5 smaller, 6 spot			
		♂ Holotype	Above	F.		Large 1b, 2-5, large 6, 7-8	9-10		
				H.	Faint 2-4	1c, prs. 2-3, 4-6			
			Below	F.	1b, prs. 2-6, 7	Pr. 1b, 2-8	2-6 : 9-10	+ with accessory	
				H.	1b, prs. 1c-5, 6	Prs. 1c-3, 4-7	1b, pr. 1c, 2-5 : 7-8	+	
		♂ Max.	Above	F.	Minute 8 on R.	Large 1b, 2-5, large 6, 7-8	9-10		
				H.	1b, prs. 2-5, 6	1b, prs. 1c-3, f. prs. 4-5, 6-7	8		
			Below	F.	1b, prs. 2-6, 7-8	Pr. 1b, 2-8	Elongated 2-6 : 9-10	Elongate doubled	
				H.	1a, 1b, prs. 1c-6, tr. 7	1b, prs. 1c-3, 4-7	Linear 1b, pr. 1c, 2-5, linear 6, rounded 7-8	+ with accessory	
		♂ Min.	Above	F.		Large 1b, 2-5, large 6	9-10		
				H.	Trs. 3-4	1c, prs. 2-3, 4-6			
			Below	F.	1b, prs. 2-4, 5-6	1b-6	2-3 : tr. 5 : 10		
				H.	1b, prs. 1c-5, 6	Prs. 1c-3, 4-7	Tr. 1c, 2-5		
		♀ Allotype	Above	F.		Large 1b-6, min. 7-8	Tr. streak 1b, large 2, 3 : tr. 9, 10	Small	
				H.		Small prs. 2-3, 4-6	Large 1c-2, 3-5	Small	
			Below	F.	Prs. 1b-4, 5, faint pr. 6, 7	1b-7, min. 8	Large 2, 3-4, min. 9, large 10	Large doubled	
				H.	1b, prs. 1c-5	Prs. 1c-3, 4-7	1b, pr. 1c, 2-5 : 7-8	Minute	
		♀ Max.	Above	F.		Large 1b-6, min. 7-8	1b, large 2, 3-6 : tr. 9, 10	+	
				H.	1a	1b, prs. 1c-3, 4-6	1b, 1c, pr. 2, 3-5	Small	
			Below	F.	Prs. 1b-6, 7	1b-7, min. 8	1b-6 : 9-10	Large	
				H.	1b, prs. 1c-6	Prs. 1c-3, 4-7	1b, pr. 1c, 2-8	Doubled	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above { F. H.		Large 1b-6, trs. 7-8 Small prs. 2-3, 4-6	2-3 : 10 1c-4	+ Small
			Below { F. H.	Prs. 1b-4, 5, ft.pr. 6, 7	1b-7, min. 8 Prs. 1c-3, 4-7	2-4 : 10 1b, pr. 1c, 2-5 : 7-8	+ Minute
103	<i>mangolinella</i>	♂ Allotype not designated					
		♂ Max.	Above { F. H.	1c, prs. 2-5, 6	Large patch 1b, 2-5, large 6, 7, tr. 8 Prs. 1c-3 fused to form a patch, large 4-5, 6	Tr. 3 : tr. 9, 10	
			Below { F. H.	Prs. 1b-6, 7 1b, prs. 1c-6, 7	Pr. 1b, 2-7, tr. 8 Prs. 1c-3, 4-7	2-6 : 9-10 Streak 1b, pr. streaks 1c, 2-5 : 7-8	Doubled Streak with accessory
		♂ Min. grades into <i>pyres pyres</i>					
		♀ Holotype	Above { F. H.		1b-6, min. 7 Small. Prs. 1c-3, 4-6	Long streak 1b, 2 fills basal half of the area, 3, streaks in 4-6 and 9, 10 The spots form a central white patch with cell	Very large
			Below { F. H.	Prs. 1b-7 1b, prs. 1c-6	1b joined to D1b, 2-6, min. 7-8 Prs. 1c-3, 4-7	Very large. 1b-6 : 9-10 Long streaks 1b and pair 1c, large 2-8	Much enlarged Almost fills cell
		♀ Max.	Above { F. H.		1b, small prs. 1c-3, 4-7, min. 8 Irregular 1c-4	Very large 2-4, 5-6, tr. 7 : 9-10 Streaks 1a-1b, two contiguous streaks 1c, very large 2-3 filling basal half each area, large 4-6, small 7	Much enlarged Fills three- quarters cell
			Below { F. H.	Prs. 1b-6, 7 1b, prs. 1c-6, 7	Pr. 1b, 2-8 Prs. 1c-3, 4-7	Very large 2-3, 4-6 : 9-10 Streaks 1a, 1b, two contiguous streaks 1c, 2-8	Very large Fills three- quarters cell
		♀ Min.	Above { F. H.		1b-7 Small prs. 2-3, 4-7	1b-3 : 9-10 Streaks 1a-1b, pair streaks 1c, 2-5, tr. 6	+ Fills half cell
			Below { F. H.	1b, prs. 2-3, 4 Prs. 1c-4	1b-6 Prs. 1c-3, 4-7	1b-6 : tr. 9, 10 Streak 1b, pr. streaks 1c, 2-8	Large Fills half cell
104	<i>paucinotata</i>	♂ Holotype	Above { F. H.		Very small 1b-3, trs. 4-5, large 6, 7 Prs. 1c-3, 4-7		
			Below { F. H.	Minute 1b, prs. 2-4, 5 Prs. 1c-5, 6	Minute 1b, 2-3, min. 4-5, 6 Prs. 1c-3, 4-7	Trs. 2-3 : tr. 10 1c elongated, 2-5 : 7-8	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
105	<i>jamesi</i>	♂ Max.	Above {	F.	1b-6, tr. 7	Tr. 9, 10	
				H.	Prs. 1c-3, 4-7		
			Below {	F. Minute 1b, prs. 2-4, 5, pr. 6, 7	Minute 1b, 2-6	Elongated 2-6 : tr. 9, 10	Doubled
				H. 1b, prs. 1c-6	Prs. 1c-3, 4-7	Streak 1b, pr. streaks 1c, 2-5 : 7-8	Large
		♂ Min.	Above {	F.	Trs. 1b-2 : trs. 5-6		
				H.	Small prs. 2-3, 4-7		
			Below {	F. 1b, prs. 2-3, 4	2-6	Trs. 2-3 : small 10	
				H. 1b, prs. 1c-6	Small prs. 1c-3, 4-7	Small streak 1c, small 2-5 : small 7	
		♀ Allotype	Above {	F.	Tr. 1b, 2	Tr. 2 : 10	
				H.	Minute prs. 2-3, 4-6	Large 1c-2, very small 3-4	
			Below {	F.	Small 1b-6	2-3 : small 10	
				H. 1b, prs. 1c-6	Small prs. 1c-3, 4-7	Pr. streaks 1c, 2-5 : 7, tr. 8	
		♂ Holotype	Above {	F.	2-5, larger 6-7		
				H.			
			Below {	F. Prs. 2-6, 7	Small 3-4, larger 5-6		
				H. Minute 2, prs. 3-4, 5	Minute 4-6		
		♂ Max.	Above {	F.	1b-8		
				H.	4-6		
			Below {	F. Prs. 1b-6, 7	Minute 2, 3-8	Minute 10	
				H. 1a, prs. 1b-5, 6	Prs. 2-3, 4-7		
		♂ Min.	Above {	F.	4-7		
				H.			
			Below {	F. Trs. 4-5	4-7		
				H.			
		♀ Allotype	Above {	F.	1b-8		
				H.	5-6		
			Below {	F. prs. 1b-7	1b-8		
				H. 1b, prs. 1c-5	4-6		
		♀ Max.	Above {	F.	1b-8		
				H. Faint 3-4	Pr. 3, 4-7		
			Below {	F. Large prs. 1b-7	1b-8	10	
				H. 1b, prs. 1c-5, 6	Prs. 1c-3, 4-7		
		♀ Min.	Above {	F.	4-8		
				H.			
			Below {	F. 1b-3, prs. 4-6, 7	4-8		
				H. Minute 3, pr. 4, 5	Minute 4-6		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
106	<i>phokion</i>	♂ Lecto-holotype	Above {	F.	4-5, large 6, 7, small 8		
				H.	Faint 5 (R. only) 6		
			Below {	F. Prs. 2-6, 7	Minute 3, 4-7		
				H. Irregular traces	Minute 5, 6, tr. 7		
		♂ Max.	Above {	F.	Pr. 1b, 2-5, large 6-7, small 8	Tr. 10	
				H.	4-6		
			Below {	F. Prs. 1b-7	Minute 2, 3-8	10	
				H. 1b, prs. 1c-5, 6	Prs. 2-3, 4-7		
		♂ Min.	Above {	F.	4-5, larger 6-7		
				H.			
			Below {	F. Tr. 1b, small prs. 2-5	4-7		
				H. Small prs. 1c-4, 5	Minute 4-6		
		♀ Lecto-allotype	Above {	F. Faint, 1b, prs. 2-6, 7	Tr. 3 on L., 4-5, large 6, 7-8		
				H.	Trs. 4-6		
			Below {	F. Prs. 1b-6, 7	4-5, large 6, 7-8		
				H. Small prs. 1c-5	4-6		
		♀ Max.	Above {	F.	1b-8		
				H.	Tr. pr. 2, pr. 3, 4-6, faint 7		
			Below {	F. Large prs. 1b-7	1b-8	10	
				H. 1b, prs. 2-6, 7	Minute pr. 1c, prs. 2-3, 4-7		
		♀ Min.	Above {	F.	2-7		
				H.	4-6		
			Below {	F. Small prs. 1b-6	4-7		
				H. Prs. 1c-5	4-6		
107	<i>salpinxoides</i>	♂ Holotype	Above {	F.	Small, 4 : 6-7		
				H.			
			Below {	F. Irregular, 2-5	Minute 4-6		
				H. Prs. 1c-5, 6	4-6, minute 7		
		♂ Max.	Above {	F.	Small 3-5, 6-7		
				H.	Small 4-6		
			Below {	F. Minute 1b, prs. 2-6, 7	4-7		
				H. Minute 1b, prs. 1c-5, 6	2, pr. 3, 4-7		
		♂ Min.	Above—F. H.				
			Below—F. H.				
		♀ Allotype	Above {	F.	Small 4-5 : tr. 7		
				H.	Trs. 4-5, small 6		
			Below {	F. Prs. 1b-6, 7	4-5		
				H. 1b, prs. 1c-5, 6	4-6		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
108	<i>bismarckiana</i>	♀ Max.	Above {	F.	Small 4-7		
				H.	Small 4-6		
			Below {	F. Prs. 1b-6, 7	4-7	2	
				H. 1b, prs. 1c-5	4-7		
		♀ Min.		Above—F. H.			
				Below—F. H.			
		♂ Holotype	Above {	F.	Small 2-5, larger 6, 7		
				H.	Small 4-6		
			Below {	F. 1b, prs. 2-6	Small 3-7		
				H. 1c, prs. 2-5, 6	4-7		
		♂ Max.	Above {	F.	1b-8		
				H.	2, pr. 3, 4-6		
			Below {	F. 1b, prs. 2-6, 7	1b-7	6 : 9-10	
				H. Faint 1b, prs. 1c-5, 6	Small prs. 1c-3, 4-7		
		♂ Min.		Above—F. H.			
			Below {	F.			
				H. Pr. 3, trs. 4-5	4-7		
		♀ Allotype	Above {	F.	2-7, tr. 8		
				H.	4-6		
			Below {	F. Prs. 1b-6, 7	2-7		
				H. 1b, prs. 1c-5, 6	Small prs. 2-3, 4-7		
		♀ Max.	Above {	F.	1b-7, tr. 8	10	
				H.	Small prs. 2-3, 4-7		
			Below {	F. Prs. 1b-6, 7	2-7	6 : 9-10	
				H. 1b, prs. 1c-5, 6	Prs. 1c-3, 4-7		
		♀ Min.	Above {	F.	Minute 2-6		
				H.	4-7		
			Below {	F.	2-7		
				H. 3-4	4-7		
109	<i>manusi</i>	♂ Holotype	Above {	F.	2-7		
				H.	4-6		
			Below {	F. On R., 2, prs. 3-6, 7	4-7	10	
				On L., 3, prs. 4-6, 7			
				H. Prs. 1c-5, 6	4-7		
		♂ Max.	Above {	F.	2-8		
				H.	Pr. 3, 4-6		
			Below {	F. 2, prs. 3-6, 7	Very small 2-5, 6-7	10	
				H. 1b, prs. 1c-6	Faint 2, pr. 3, 4-7		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
	♂ Min.	Above	F.		4-7			
			H.		4-5			
		Below	F.	Minute prs. 3-4	4-7	10		
			H.	Irregular, 1c-5	4-7			
	♀ Allotype	Above	F.		Minute 2, small 3-5, 6-7			
			H.		4-7			
		Below	F.	Prs. 2-6, 7	Tr. 2, small 3-5, 6-7	Small 10		
			H.	1b, prs. 1c-5, 6	Small prs. 1c-3, 4-7			
	110 <i>nivani</i>	♂ Holotype	Above	F.		Large 1b-5, larger 6-7, 8	10	
				H.		Small pr. 3, 4-7		
Below			F.	1b, prs. 2-6, 7	Large 1b-5, larger 6-7, 8	Small 10		
			H.	Tr. 1b, prs. 1c-5	Prs. 2-3, 4-7			
♂ Max.		Above	F.		Large 1b-5, larger 6-7, 8	10		
			H.		Small pr. 3, 4-7			
		Below	F.	1b, prs. 2-6, 7	Large 1b-5, larger 6-7, 8	Small 10		
			H.	Tr. 1b, prs. 1c-5	Minute prs. 1c-2, pr. 3, 4-7			
♂ Min.		Above	F.		Large 1b-5, larger 6-7, 8			
			H.		4-7			
	Below	F.	1b, prs. 2-6, 7	Large 1b-5, larger 6-7, 8	Small 10			
		H.	1c, prs. 2-3, tr.pr. 4	Minute prs. 2-3, 4-6				
None available								
111 <i>callithoe</i>	♂ Holotype	Above	F.	Prs. 1b-5, 6	2-3, 4 to D4, 5-7	2-3, 4 to S4, very large 5, large 6: 9-11	+	
			H.	Irregular traces	Minute 2, 3-5			
		Below	F.	Trs. 2-3				
			H.		Trs. prs. 2-3, 4-6	Trs. 3-6		
	♀ Type not designated							
112A <i>hansemanni</i>	♂ Type not designated							
	♀ Holotype	Large whitish blue patch on F.W. just not including all the small submarginals, but including all the cell, and discals anterior to vein 2						
	Above	F.	1b, prs. 2-6	Pr. 1b, 2-3 lost in main patch, small 4-7	1b elongated and forming two patches. The rest included in main patch	Patch		
		H.	Tr.pr. 1c, prs. 2-6	Ft.pr. 1c, prs. 2-3, 4-6	2-5	Trace		
	Below	F.	White patch where blue above	Small prs. 2-3, 4	Small 2			
H.		Irregular 2-4	Very small prs. 2-3, 4-6	3-7 (linear)				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
112B	<i>durrsteini</i>	♂	Type not designated					
		♀	Type (from figure)					
			Above	{ Large whitish-blue patch on F.W. from vein 2 and round apex to vein 12. The only spot is D1b. H.W. above is broadly whitish to end of cell which is brown, the bases of areas 1a, 1b, 1c brown. No spots				
			Below	{ F. The same whitish patch, extending back through distal parts of 1a and 1b to the inner margin. Small D1b H. Uniform brown except for spots in D4, 5, 6 and in cell				
113	<i>admiralia</i>	♂	Type not designated					
		♂ Max.	Above	{ F. 1b, prs. 2-6, 7 H. 2, prs. 3-6	Pr. 1b, 2-8 (3 to D3) Prs. 2-3, 4-6	2-6 (3 to D3) : 9-11 2-5	+ +	
			Below	{ F. 1b, prs. 2-6, 7 H. Prs. 2-4, trs. 5-6	Very small 1b-8 Tr. 1b, prs. 1c-3, 4-7	2-5 2-6	Trace	
		♂ Min.	Above	{ F. 1b, prs. 2-6 H.	1b-7 Pr. 3, 4-6	2-6 : 9-11 Minute 2-3	Trace	
			Below	{ F. Prs. 2-3 : 6 H.	1b-2 : 6-7 4-6	2-3, faint 4 Minute 2-3		
		♀ Holotype	Above	{ F. Large prs. 1b-4, prs. 5-6 H. Prs. 2-6	Pr. 1b, 2-3 to D2-3, 4-8 Prs. 1c-3, 4-6	1b oval with accessory, 2-3 to S2-3, 4-6 fused : 9-11 Pr. 1c, 2-6	Large with accessory	
			Below	{ F. 1b, prs. 2-6 H. 1b, prs. 1c-6	1b-8, tr. 9 1b, prs. 1c-3, 4-7	Large 1b-5, tr. 6 : tr. 9, large 10 Pr. 1c, 2-7	Small Trace	
		♀ Max.	Above	{ F. Prs. 1b-7 H. Prs. 2-6, 7	Pr. 1b, 2-6 (3 meets D3) : 8 Pr. 1c, 2-7	1b-6 (3 meets S3) : 9-11 1c-6	+	
			Below	{ F. 1b, prs. 2-7, 8 H. Prs. 1b-6	Pr. 1b, 2-8 (3 meets D3) Pr. 1c, 2-7	1b-6 (3 meets S3) : 9-11 1c-6, tr. 7	+ +	
		♀ Min.	Above	{ F. Small and irregular H. Small and irregular	Pr. 1b, 2-8 Pr. 1c, 2-6	1b-6 : 9-11 1c-5	+	
			Below	{ F. 1b, prs. 2-6, 7 H. Small and irregular	1b, 2-8 Pr. 1c, 2-6	1b-6 : 9-10 1c-5	Very small	
114	<i>eurykleia</i>	♂	Holotype	Above	{ F. 1b, prs. 2-3, 4 H.	Small 1b, 2-3 to D2-3, 4-6 2-5	Small 1b, 2-3 to S2-3, 4-6 : 9-11 confluent 2-4, tr. 5	Two joined by neck Trace
			Below	{ F. H.		Large 2-3 Trace 2-4	Trace	
		♂ Max.	Above	{ F. Prs. 1b-4, 5-7 H. Prs. 2-5, 6	Pr. 1b, 2 to D2, 3-6 to discal patch, small 7-8 Small prs. 2-5, 6 lost in costal patch	1b, 2 to S2, 3-11 with cell form confluent patch 2-5, 6 lost in costal patch	+ Very small	
			Below	{ F. 1b, prs. 2-3, 4 H. 1c, prs. 2-6	1b-3 : 6 Prs. 2-3, 4-6	2-5 : 10 2-7	+ Small	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell	
115	<i>arova</i>	♂ Min.	Above	F.	1b-3	Tr. 1b, 2, 3 meets D3, small 4-6	Small 1b, 2, 3 meets S3, 4-6 : 9-11 almost confluent	+
				H.		Minute 5-6	Small 2-4	
			Below	F.			2-3	
				H.			Trs. 2-4	
		♀ Allotype	Above	F.	Faint traces	Faint 2-7	Small 1b. Remaining D. with cell form patch filling wing anterior to vein 2	+
				H.	Faint prs. 1b-6	Prs. 1c-3, 4-6	1c-5	Trace
			Below	F.	Faint traces	Faint 2-6	Small 1b : large patch as above	+
				H.	Prs. 1c-4	Faint prs. 1c-3, 4-6		Trace
		♀ Max.	Above	F.	Prs 1b-6, 7	Pr. 1b, 2-4 to D. 2-4, 5-8	1b : all others with cell form large patch	+
				H.	Prs. 1c-6	Prs. 1c-3 to D., 4-5 to D., 6 lost in costal patch	1c-5 to S., 6 forms a costal patch	Small
			Below	F.	Traces	Faint 2-6	1b, and patch as above	+
				H.	Prs. 1c-6	Prs. 1c-3, 4-6		+
	♀ Min.	Above	F.	Faint traces	Faint 2-7 (2-3 to D. 2-3)	Small 1b, 2-3 to S 2-3, 4-6 : 9-11 not confluent	+	
			H.	Faint prs. 2-6	1c, prs. 2-3, 4-6	Trs. 1c, 2-6		
		Below	F.		Minute 6	1b-4 : minute 10	Trace	
			H.	Irregular traces	Tr. 6	3-6		
		♂ Holotype	Above	F.	Pr. 1b-5	Pr. 1b, 2-3 to D. 2-3, 4 meets D4, 5-7	1b, 2-3 to S. 2-3, 4-6 with 9-11 confluent	Large
				H.	Faint prs. 3-5	3-6	2-5	Minute
			Below	F.			2-4	Trace
				H.	Traces	Irregular traces	Minute 2, small 3-7	
			♂ Max.	Above	F.	Prs. 1b-5, 6	Pr. 1b, 2-4 to D. 2-4, 5-8	1b, 2-4 to S. 2-4, large 5-6 with 9-11
H.					Prs. 2-6	2, pr. 3, 4-6	2-5	Small
Below		F.			Small 1b-3	2-4, tr. 5	Trace	
		H.		Prs. 3-6	Prs. 2-3, 4-6	2-5	Small	
♂ Min.		Above	F.	Prs. 1b-3	Pr. 1b, 2-3 meet D. 2-3	1b, 2-3 to S. 2-3, 4-6 and 8-10 not confluent	+	
			H.	Faint prs. 3-5	3-6	2-5		
		Below	F.			2-3		
			H.	Tr. 4	Minute 5-6	Small 3-5		
♀ Type not designated								
♀ Max.		Above	F.	Prs. 1b-6, 7	Pr. 1b, 2-3 to D. 2-3, 4-8	1b, 2-3 to S. 2-3, 4-6 : 8-11	+	
			H.	1c, prs. 2-6	Prs. 1c-3, 4-6	1c-7	+	
		Below	F.	Irregular traces	1b-3, min. 4 and 6	1b-5, tr. 6 : trs. 9-10	Large with accessory streak	
			H.	Prs. 1c-6	Prs. 1c-3, 4-7	1c-7	+	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell			
116	<i>unibrunnea</i>	♀ Min.	Above	{ F. Prs. 1b-3, 4-6 H. Prs. 2-6	Pr. 1b, 2-3 to D. 2 3, 4-7 Prs. 2-3, 4-6	1b, 2-3 to S. 2-3, 4-6 : 8-10 1c-5	Large			
		Below	{ F. Irregular traces H. Prs. 1c-4, 5-6	1b-3 : 6 Prs. 2-3, 4-6	1b-5 : 10 3-6, tr. 7					
		♂ Holotype	Above—F. H.							
		Below	{ F. 3-4 H. 1c-2, prs. 3-5, 6	2, tr. 3, small 4-8 Small 4-6	Large 2-3 1c-7 (1c and 3 very small)	Trace Small				
		♂ Max.	Above	{ F. H.	Small 4-8					
		Below	{ F. 1b, prs. 2-3, small prs. 4-6 H. 1c, prs. 2-6	1b, prs. 2-3, 4-8 1b with streak, prs. 1c-3, 4-6, tr. 7	Small 1b, large 2-3, tr. 4 : tr. 10 1c with streak, 2-7	Large +				
		♂ Min.	Above—F. H.							
		Below	{ F. 4 H. 4	2, tr. 3, very small 4-8 Minute 4-6	2-3 4-7	Trace Trace				
		♀ Max.	Above	{ F. H. Prs. 1c-5	Faint 5-8 Prs. 1c-3 : 5	Large 1b-3 2-5				
		Below	{ F. 1b, prs. 2-6, 7 H. 1b, prs. 1c-6, tr. 7	1b-8, tr. 9 S. and D. linked by white streaks. 1b, prs. 1c-3, 4-7	1b-4, tr. 5 : tr. 10 Pr. 1c, 2-7	+				
		♀ Min.	Above—F. H.							
		Below	{ F. 3-4 H. Prs. 3-6	1b-8 Prs. 1c-3, 4-6	1b-3 1c-7	+				
		117	<i>browni</i>	♂ Holotype	Above—F. H.					
				Below	{ F. 2-6 H.	Faint 5-7, 8		+		
				♂ Max.	Above—F. H.					
				Below	{ F. 2-6 H.	Faint 5-7, 8		+		
♂ Min.	Above—F. H.									
Below—F. H.										
♀ Type not designated										
♀ Max.	Above—F. H.									
Below	{ F. 1b, prs. 2-7 H. Prs. 1c-6, 7			2-8 Prs. 1c-3, 4-7	1b-4 1c-7	+				
♀ Min.	Above—F. H.									
Below—F. H.										

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell			
118	<i>heurippa</i>	♂ Holotype	Above	F.	Small 2-7	9-10				
				H.	Tr. 5	Tr. 3, small 4				
			Below	F.	3-4 on L., pr. 3, 4 on R.	Minute 1b, 2-8	Small 1b, large 2-3, 4-9	Large		
				H.		1b, prs. 1c-2, 3-6	2-7	Small		
		♂ Max.	Above	F.	2-7, tr. 8	2, 3-6 streaks : 9-10	Large dyslegnic			
				H.	Small 3-4. White suffusion masks 5-6	2-4, 5 dyslegnic. White suffusion fills 6-7				
			Below	F.	Prs. 3-5, 6-7	Small pr. 1b, 2-8	1b-6 : 9	Large		
				H.	Prs. 1c-5, 6	1b, prs. 1c-3, 4-6, tr. 7	Tr. 1c, 2-7	Small		
		♂ Min.	Above—F. H.							
			Below	F.			Small 1b, large 2-3	+		
				♀ Allotype	Above	F.	Small 2-7	9-10		
						H.		2-5	Trace	
					Below	F.	Pr. 3, 4	1b-8	1b-5 (4-5 very small) : 9	Large
						H.	Small and irregular	1b, prs. 1c-3, 4-7	1c-7	Small
♀ Max.	Above			F.	Tr. 1b, 2-7, tr. 8	9-10				
				H.	Traces 1b, prs. 2-3, faint 4-6	Tr. 1c, 2-5	Trace			
	Below			F.	1b, prs. 1c-6, 7	Pr. 1b, 2-8	1b, large 2-3, 4-6 : 9	Large		
				H.	1b, prs. 1c-5, 6	1b, prs. 1c-3, 4-7	1c-7	Small		
♀ Min.	Above—F. H.									
	Below			F.	4	1b-7	Tr. 1b, large 2-3 : tr. 9	+		
	H.			Irregular traces	1b, prs. 1c-3, 4-6	2-6				
119	<i>kadu</i>			♂ Type not available						
				♂ Max.	Above	F.	2 : trs. 6-7	1b-8, tr. 9	Very large 1b, 2 : 10, tr. 11	
						H.		3-7		
			Below	F.	1a, prs. 1b-7	Tr. 1b, 2, small 3-5, 6-8	Very large 2, tr. 3, 4 : 10, tr. 11			
				H.	1b, prs. 1c-6	Prs. 1c-3, 4-7				
		♂ Min.	Above	F.		4-7	1b			
				H.		Small 4-5				
			Below	F.	Tr. 6, pr. 7	Tr. 2 : small 6-7	2			
				H.	Irregular traces	Trs. prs. 2-3, small 4-7				
		♀ Type not available								
		♀ Max.	Above	F.	Trs. 6-8	1b-9	1b-2 : 10-11			
				H.	Minute prs. 2-3, 4	Prs. 2-3, 4-6				
			Below	F.	Prs. 1b-7, tr. 8	Tr. 1b, 2, small 3-5, 6-8	Large 2, small 3-4 : small 10-11			
				H.	1b, prs. 1c-6	Prs. 1c-3, 4-7				

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above { F. H.		2 : 4-7 Pr. 3, 4-6	2 : tr. 10	
			Below { F. H.	1b-2 : 5, prs. 6-7 1b, prs. 1c-4	2 : 6-8 Faint pr. 2, tr. pr. 3, 4		
120	<i>custachius</i>	♂ Holotype	Above { F. H.		Very small 2, 3-8 Tr. 6	Tr. 10	
			Below { F. H.	7, and tr. pr. 6 on L.	2-8 Small 3-7	2 : 10	
		♂ Max.	Above { F. H.		1b-9 Small 3-6	Tr. 10	
			Below { F. H.	1b, prs. 2-7 (6-7 to S.) 1b, prs. 1c-5, 6	Small 1b, 2-8 (6-7 to A.), small 9 Small prs. 1c-3, 4-7	2 : 10	
		♂ Min.	Above { F. H.		Very small 2-5, 6-7		
			Below { F. H.			2	
		♀ Max.	Above { F. H.	Tr. 3 2, prs. 3-5, 6	1b-8, tr. 9 Prs. 2-3, 4-7		
			Below { F. H.	Prs. 1b-7 (6-7 to S.) 1b, prs. 1c-6, tr. 7	Pr. 1b, 2-8 (6-7 to A.) 1c, prs. 2-3, 4-7	1b-2 : 10	
		♀ Min.	Above { F. H.		2 : 4-7, tr. 8		
			Below { F. H.		Minute 6-7	2	
121	<i>aviena</i>	♂ Type not available					
		♂ Max.	Above { F. H.	Trs. 2-3 2, prs. 3-5, 6	1b-8 Small pr. 3, small 4-7	Small 10	
			Below { F. H.	1b, prs. 2-7 (6-7 to S.) 1b, prs. 1c-6	2-8 (6-7 to A.) Prs. 2-3, 4-7	2 : tr. 10	
		♂ Min.	Above { F. H.		3-8		
			Below { F. H.		4-8	2	
		♀ Type not available					
		♀ Max.	Above { F. H.		Small 1b, 2-8, tr. 9 Tr. pr. 2, pr. 3, 4-6	Small 10	
			Below { F. H.	1b, prs. 2-7 (6-7 to S.) 1b, prs. 1c-6	1b-8 (6-7 to A.) Small prs. 2-3 4-7	2 : 10	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
122	<i>erima</i>	♀ Min.	Above { F. H.		2-8 Small 6		
			Below { F. H.		2-8 4-6	2	
		♂ Holotype	Above—F. H.				
			Below { F. H.			Minute 2	
		♂ Max.	Above { F. H.		2-7		
			Below { F. H.		2-8 4-7	2 : 10	
		♂ Min.	Above—F. H. Below—F. H.				
		♀ Allotype	Above—F. H.				
			Below { F. H.			2	
					Small 4-7		
		♀ Max.	Above { F. H.		Minute 4-7 Faint 4-6		
			Below { F. H.		Small 3-7 4-7	2 : 10	
		♀ Min.	Above—F. H.				
			Below { F. H.			Faint 2	
123	<i>rhodia</i>	♂ Type not available					
		♂ Max.	Above { F. H.		Very small 2-8	Tr. 10	
			Below { F. H.		2-8 Small prs. 1c-3, 4-7	2 : 10	
		♂ Min.	Above—F. H.				
			Below { F. H.		Small 5-7	2	
		♀ Type not available					
		♀ Max.	Above { F. H.		Tr. 6 one side only 4-7		
			Below { F. H.		Minute 2, 3-8 Small pr. 1c, prs. 2-3, 4-7	Large 2 : 10	
		♀ Min.	Above { F. H.		Minute 4, 5-6		
			Below { F. H.		Small 5 Very small 4-5, 6-7	Large 2 : small 10	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
124	<i>messia</i>	♀ Lectotype	Above { F. H.		Small 5-6 4-7		
			Below { F. H.		Tr. 3, 4-8	1b (a spot in front of the white area), large 2 : large 10	
125	<i>affinita</i>	♂ Type not designated					
		♂ Max.	Above { F. H.		2-7, tr. 8 4-7	Large 1b with accessory, tr. 2 : large 10, streak 11	
			Below { F. 2 : pr. 6 H. 1b, prs. 1c-5		2-8 Prs. 2-3, 4-7	2, small 3 : streak 9, large 10	
		♂ Min.	Above { F. H.		Tr. 3, 4-7, tr. 8 5-7	Tr. 10	
			Below { F. H.		3-8 2 on one side only, pr. 3, 4-7	2 : 10	
		♀ Holotype	Above { F. H.		2-7, tr. 8 Prs. 2-3, 4-7	Large 10	
			Below { F. 1b, prs. 2-6, 7 H. Prs. 1c-5		2-8 Prs. 2-3, 4-7	1b, 2 : 10	
		♀ Max.	Above { F. H.		2-8 Small prs. 2-3, 4-7	Large 1b, 2 : 9-10	
			Below { F. 1b, prs. 2-6, 7 H. Pr. 1b, 1c, prs. 2-5, 6		Minute 1b, 2-8 Minute 1c, prs. 2-3, 4-7	2-3 : str. 9, 10	
		♀ Min.	Above { F. H.		2-8 4-7	1b : 10	
			Below { F. H.		2-8 Minute prs. 2-3, 4-7	2 : 10	
126	<i>perdita</i>	♂ Holotype	Above { F. H.		Minute 2, 3-7, tr. 8		
			Below { F. H.		2-8 Minute prs. 2-3, 4-7	2 : 10	
		♂ Max.	Above { F. H.		2-7, min. 8 4-7	10	
			Below { F. 1b, prs. 2-7 H. Tr. 1b, prs. 1c-5, 6, tr. 7		2-8 Prs. 1c-3, 4-7	2, small 3 : 10	
		♂ Min.	Above—F. H.				
			Below { F. H.		Small 6-8 5-7	2	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
127	<i>pulchella</i>	♀ Allotype	Above { F.				
			H.		Small 4-6		
			Below { F.		4-8	Small 2 and 10	
			H.		Prs. 2-3, 4-7		
		♀ Max.	Above { F.		2-8	3 : large 10	
			H.		Tr. pr. 3, 4-7		
			Below { F.	1b, prs. 2-3, irregular 4-6	2-8	Large 2, small 3 : large 10	
			H.	1b, prs. 1c-5	Minute prs. 1c-3, 4-7		
		♀ Min.	Above { F.		Small 5-6		
			H.		Very small 5-6		
			Below { F.		Small 5-6	2	
			H.		5-7		
		♂ Holotype	Above { F.		2-7, tr. 8		
			H.		6		
			Below { F.		2-8	2 : 10	
			H.	Minute 3-4	Prs. 2-3, 4-7		
		♂ Max.	Above { F.		2-8	Tr. 10	
			H.		4-7		
			Below { F.	1b, prs. 2-6, 7	2-8	2 : 10	
			H.	Prs. 1c-4, 5	Prs. 1c-3, 4-7		
		♂ Min.	Above { F.		6		
			H.		7		
			Below { F.		Trs. 2-4 : 6	Tr. 2	
			H.		Pr. 3, 4-6		
		♀ Allotype	Above { F.		2-7, tr. 8	Tr. 10	
			H.		4-6		
			Below { F.		2-8	2 : 10	
			H.	Minute 2, prs. 3-4	1c, prs. 2-3, 4-6		
		♀ Max.	Above { F.		2-8	10	
			H.		4-7		
			Below { F.	1b, pr. 2	2-8	2 : 10	
			H.	2, prs. 3-4	1c, prs. 2-3, 4-7		
		♀ Min.	Above { F.		6		
			H.		Trs. 5-6, small 7		
			Below { F.		2-8	Tr. 2	
			H.		Minute prs. 2-3, 4-7		
128	<i>polymela</i> (Pl. 5, fig. 6)	♂ Holotype	Above—F. H.				
			Below { F.		Small 2-8	2 : 10	
			H.	Minute traces	Prs. 2-3, 4-7		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
	♂ Max.		Above { F. H.		2-7 Minute 5-6		
			Below { F. 1b, tr. 2, pr. 3, 4-6 H. Prs. 1c-4		2-8 Small prs. 1c-3, 4-7	2-3 : 6 : 10-11	
	♂ Min.		Above—F. H.				
			Below { F. H.		Very small 6 and 8 Minute 4-6		
	♀ Allotype		Above { F. H.		4-6		
			Below { F. H.		2-8 Prs. 2-3, 4-7	2-3 : 10	
	♀ Max.		Above { F. H.		2-8 Prs. 2-3, 4-7	Tr. 10	
			Below { F. H. Trs. 2-4		2-8 Prs. 1c-3, 4-7	2-3 : 9-10	
	♀ Min.		Above { F. H.		Trs. 5-7		
			Below { F. H.		Minute 8 Small 4-6	2 : 10	
129	<i>imitata</i> (Pl. 8, fig. 4)	♂ Holotype	Above { F. H.		Faint 2-3 2-5	10	
			Below { F. H.		Faint 2-3 Small, pr. 3, 4-7	2 : 10	
	♂ Max.		Above { F. H.		2-3 2-5, tr. 6	10	
			Below { F. Prs. 2-3 H.		2-5 Small prs. 2-3, 4-7	2 : 10	
	♂ Min.		Above { F. H.			10 free	
			Below { F. H.		Trs. 5-6 Minute 4-6	2 : 10	
	♀ Type not designated						
	♀ Max.		Above { F. H.			Faint 10	
			Below { F. H.		Faint 5-7 2 6-7	2 : 10, tr. 11	
	♀ Min.		Above—F. H.				
			Below { F. H.			2 : 10	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
130	<i>rossi</i> (Pl. 5, fig. 3)	♂ Holotype	Above { F. H.	1b f.pr. Ads. 1b-5 prs. blended with S1b-5. smaller S6	2-8 a row of varied size, tr. 9		
			Below { F. H.	Ads. prs. 1b-6 linked to S1b-6, S7-8 Single Ad. 7 1b and prs. 1c-4 linked to S., min. pr. 5	F.pr. 1b, pr. 1c, f.pr. 2-4, 5-7	2 : 10	
131	<i>crucis</i>	♂ Holotype	Above { F. H.		Trs. 6-7	Tr. 10	
			Below { F. H.		Tr. 3, small 4-8 Small 4-7	2 : 10	
		♂ Paratype A	Above { F. H.		6, trs. 7-8	Tr. 10	
			Below { F. H.		4-8 Tr. 3, small 4-7	Large 2 and 10	
		♂ Paratype B	Above { F. H.		6-7	? (much rubbed)	
			Below { F. H.		Small 4-5, 6-8	2 : very small 10	
		♀ Allotype	Above { F. H.		Faint 4-8 Faint. Small prs. 2-3, 4-7		
			Below { F. H.		Faint 4-7 Faint. Small prs. 2-3, 4-7		
132	<i>eustachiella</i>	♂ Holotype	Above { F. H.		4-8	10	
			Below { F. H.		3-8 Prs. 2-3, 4-6	2 : 10	
		♀ Allotype	Above { F. H.		4-8 Faint prs. 2-3, 4-7	Large 10	
			Below { F. H.		Small 4-8 Prs. 2-3, 4-7	2 : 10	
		♀ Paratype	Above { F. H.		3-8 Faint prs. 2-3, 4-7	10	
			Below { F. H.		Small 3-8 Prs. 2-3, 4-7	2 : 10	
133	<i>iphianassa</i>	♂ Holotype	Above { F. H.		3-8	10	
			Below { F. H.		Minute 2, 3-8 2, pr. 3, 4-7	Large 2 : 10	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♂ Max.	Above { F. H.		2-9 Trs.prs. 2-3, 4-7	Base of 6 : 9-10	
			Below { F. H.		1b-8 Prs. 1c-3, 4-7	2 : 10	
		♂ Min.	Above { F. H.		4-8		
			Below { F. H.		4-8 Minute 3-4, 5-6	2 : 10	
		♀ Allotype	Above { F. H.		2-8 Prs. 2-3 show through, 4-6	10	
			Below { F. H.		2-8, tr. 9 Prs. 2-3, 4-7	Small 1b, 2 : 10	
		♀ Max.	Above { F. H.		1b, large 2-8 Tr. pr. 1c, prs. 2-3, 4-7	Tr. 6 : tr. 9, 10	
			Below { F. H.	Prs. 2-3, 4	Large 2-8 Prs. 1c-3, 4-7	1b-2 : tr. 6 : tr. 9, 10	
		♀ Min.	Above { F. H.		4-8 4-6		
			Below { F. H.		Minute 2 : 4-8 Minute pr. 1c, prs. 2-3, 4-6	2 : 10	
134	<i>novarum-ebudum</i>	♂ Holotype	Above { F. H.		2-8 2-3 show through, small 4-6	10	
			Below { F. H.		2-8 Prs. 1c-3, 4-7	10	
		♂ Max.	Above { F. H.		2-8 Faint 2-3, 4-6	6 : 9-10	
			Below { F. H.	Sparse and irregular	2-8 Prs. 1c-3, 4-7	2 : small 6 : small 9, 10	
		♂ Min.	Above { F. H.		Minute 4-5, 6-7, min. 8		
			Below { F. H.		4-8 Trs. prs. 2-3, 4-7	2 : 10	
		♀ Type not designated					
		♀ Max.	Above { F. H.		Large 2-8 (6-7 confluent) Large pr. 1c, prs. 2-3, 4-6	9-10	
			Below { F. H.		Large 2-8 (6-7 confluent) 1b, 1c, prs. 2-3, 4-7	2 : 10	

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above { F. H.		Faint 2-7 Prs. 2-3, 4-6	10	
			Below { F. H.		2-8 Prs. 2-3, 4-7	2 : 10	
135	<i>macleayi</i> (aberration Pl. 9, fig. 4)	♂ Type not designated					
		♂ Max.	Above { F. H.		2-8 Prs. 1c-3, 4-7	Pr. 2 : 6 : tr. 9, 10	
			Below { F. H.	1b, prs. 1c-4	2-8 Prs. 1c-3, 4-7	Pr. 2 : 6 : 9-10, tr. 11	
		♂ Min.	Above { F. H.		3-8 5-7	10	
			Below { F. H.		2-8 Tr. pr. 2, pr. 3, 4-7	2 : 10	
		♀ Holotype	Above { F. H.		2-8 1c, prs. 2-3, 4-6	10	
			Below { F. H.		2-8 Prs. 1c-3, 4-7	Large 2 : 10	
		♀ Max.	Above { F. H.		2-8 Prs. 2-3, 4-7	9-10	
			Below { F. H.	1b, prs. 1c-4	Small 1b, 2-8 Prs. 1c-3, 4-7	2 : 10	
		♀ Min.	Above { F. H.		4-8 4-7	Tr. 10	
			Below { F. H.		3-8 Prs. 2-3, 4-7	2 : 10	
136	<i>usipetes</i>	♂ Holotype	Above—F. H. Below—F. H.				
		♂ Max.	Above { F. H.		Small 2-7		
			Below { F. H.		Tr. 2 Tr. 6		
		♂ Min.	Above—F. H. Below—F. H.				
		♀ Type not designated					
		♀ Max.	Above { F. H.		Ill defined 2		
			Below { F. H.		2-5 Minute 4-6		

No.	Name	Example	Wings	Admarginals	Submarginals	Discals	Cell
		♀ Min.	Above—F. H. Below—F. H.				
137	<i>rezia</i>	♂ Holotype	Above { F. H. Below { F. H.		2-7 Minute 2 : 4-7, min. 8 on R. only		
		♂ Max.	Above { F. H. Below { F. H.	Minute prs. 6-7	2-8 2-8	10	
		♂ Min.	Above { F. H. Below—F. H.		2		
		♀ Allotype	Above { F. H. Below { F. H.		Pr. 1b, large 2, 3-7 Small 1b, large 2 : min. 6, 7		
		♀ Max.	Above { F. H. Below { F. H.		1b-8 2-8		
		♀ Min.	Above { F. H. Below { F. H.		2 : 6-7 Small 2		

PART 3. DISTRIBUTION AND NUMBERS.

In order to save repetition, the references to figures are not given here, but can be found from the previous section dealing with the spot pattern, under the same serial number.

No. 1, *brunnescens*.

This new subspecies differs from all other forms of *lewinii* by its light brown colour on the upper side, which is matched by Ridgway's (1912) "Prout's Brown" on his plate XV. The underside is even paler, thus differing from *lilybaea* which *brunnescens* most resembles, and the H.W. shows less differentiation between basal and peripheral areas than does *lilybaea*; the apical area of the F.W. around S.5-7 is almost unicolorous with the rest of the wing, and on the H.W. the neighbourhood of the submarginals is scarcely differentiated.

The large spot in F.W.3 is incised externally in the holotype and ten other males out of the total of thirteen. The female allotype has, on the H.W., S.2-3 more elongated than in any male, and S.4 appears as a short fused pair on the upper side

but not quite fused below. The spot in 3 on the underside of the F.W. in *brunnescens* shows the hook mentioned in the preliminary remarks: the following spots are bluish-white, the rest creamy: F.W., D.4-6 and Cell, H.W., D.1c-7 and cell.

Holotype and paratypes in the American Museum of Natural History, New York: paratypes in University Museum, Oxford, and British Museum (Nat. Hist.).

DISTRIBUTION. *Santa Cruz Isles*: Tikopia, ♂ Holotype + 11 paratypes, ♀ allotype; Vanikoro, ♂ 1. Total ♂ 13, ♀ 1.

Two males, kindly sent to me for inspection by the American Museum of Natural History, were labelled "Guadalcanar". This requires confirmation, for among very large numbers of *Euploea* from the Solomons there has been no example of any form of the *lewini* complex. It is curious that two specimens, received from the California Academy of Science, collected on Anuta or Cherry Isle in the Santa Cruz group, are not like those from Tikopia and Vanikoro, but agree better with the Fijian *eschschoitzii*.

No. 2, *lilybaea*.

General ground colour of upper side brownish, rather than black as it is in *montrouzieri*. Beneath, the mottling is not so grey as in *montrouzieri*, and there is a more strongly-marked pattern than in *eschschoitzii*, with a darker shade at the base of the H.W. extending to just beyond the discal spots, beyond which the colour is lighter.

Spot markings.—The presence of A.4 and S.4 on the F.W. is exceptional. Sub.3 is always absent in ♂: the large D.3 is generally short, almost square, and sometimes notched externally. On the H.W., S.4 may appear as a fused pair. In this, and other members of the *lewini* complex, the discal and cell spots on the underside of the H.W. are often bluish in tint. The two rows of spots on the H.W. are like those of *eschschoitzii*, being slightly larger than in *montrouzieri* and not missing from the anal end of the series as in *montrouzieri*.

DISTRIBUTION. *New Hebrides*: Espiritu Santo, ♂ 7, ♀ 2; Dolphin Island, ♂ 1; Malo, ♀ 1; Pentecost Island, ♂ 3; Efate, ♂ 1, ♀ 2; Erromanga, ♀ 2; Tana, ♂ 3, ♀ type + 1; Aneityum, ♂ 1. Total ♂ 16, ♀ 9. This form is widely distributed through New Hebrides from north to south, but none has been seen from Maewo (or Aurora), Aoba, or Ambrim and many smaller isles. It is nearest to the Fijian *eschschoitzii*.

No. 3, *montrouzieri* ("helcita" auctorum).

This subspecies, on the upper side, is of a darker, more blackish, brown than the two preceding: below it is more strongly patterned than *lilybaea*, for on the H.W. the cell, and proximal part of the anal marginal area, are as light as the band between the discals and submarginals. Some specimens have the paler areas decidedly greyish. There is usually a lack of Ads. and Subs. at the anal extremity of the rows on the upper side of the H.W.; on the F.W., S.3-4 are lacking, except for an occasional trace of 4. D.3 is approximately square. On the F.W. underside S.4-6 and 9 may be blued while other spots are white.

DISTRIBUTION. *New Caledonia*: ♂ 61, ♀ 42 (including type). I have also seen, through the kindness of the American Museum of Natural History, a specimen of *montrouzieri* purporting to come from Dolphin Island in the New Hebrides area, off the east coast of Espiritu Santo. In the absence of confirmatory evidence of this subspecies in the New Hebrides this record is regarded as doubtful. Viette (1950) figured *montrouzieri* under the old name of "*helcita*" and recorded it from the Loyalty group. Since no form of *lewinii* had previously been known from that locality I wrote to M. Viette, who kindly sent me one of the specimens. It was a female *montrouzieri* bearing data "I. Loyalty Maré Dr. R. Catala". Date of capture was not given.

Some of the subspecies of *lewinii* present points of interest when comparison is made of the degree of development of the costal spots D.10-11 of the F.W. upper surface, and of the cell-spots on the under-surface. These are tabulated as Large, Normal, Small, Trace, or Absent. For *montrouzieri* the figures are as follows for 41 specimens of males: females are not given as they are usually numerically insufficient.

Forty-one male specimens.														
F.W.									H.W.					
D.10-11 above				Cell-spot below					Cell-spot below					
	N.	S.	T.	A.	L.	N.	S.	T.	A.	L.	N.	S.	T.	A.
%	68.3	31.7	0	0	34	41.5	24.5	0	0	7.3	65.8	26.8	0	0

No. 4, *eschsoltzii*.

General ground colour slightly blacker than in *lilybaea* or even *montrouzieri*, and on the underside much less differentiated into a dark base on the H.W. Variation of the upper surface is chiefly shown on the F.W. by clouding over of the proximal end of the large D.3, but the smaller spot thus formed is not like that of *distincta* (*vide infra*) in which the distal edge of the spot is eulegmic and sharply incised by a black line. In 1b the Ads., when fused with the Sub., together with large S.2-3, form a conspicuous row leading the eye to D.10-11 on the costa. Transition to *perryi* (*vide infra*) is shown by reduction of the discals and cell-spot on the F.W. and diminution of discals on the H.W. Lengthening of the H.W. Subs. produces transitions to *walkeri* (*vide infra*).

On the F.W. A.4 is only exceptionally present as a trace in the maximal male, and S.4 is rare. On the H.W. the Ads. are not cut off at the anal end of the row. The following is the condition of the spots D.10-11 on F.W. above, and the cell-spots below, the headings are as before under *montrouzieri*; the figures are percentages.

F.W. (119 specimens)								H.W. (110 specimens)							
D.10-11 above				Cell-spot below				Cell-spot below							
N.	S.	T.	A.	N.	S.	T.	A.	N.	S.	T.	A.				
85.7	11.8	2.5	0	62.2	31.9	5	0.8	49	43.6	5.4	1.8				

DISTRIBUTION. *Western Fiji*: "Fiji" ♂ type +21, ♀ 1; Yasawa group, ♂ 4; Viti Levu, ♂ 48, ♀ 17; Ovalau, ♂ 23, ♀ 8; Vanua Levu, ♂ 14, ♀ 7; Taveuni, ♂ 6, ♀ 1; Koro, ♂ 1; Ngau, ♂ 2 +1 tr. to *walkeri*; Ono, ♀ 1 (a peculiarly brownish specimen somewhat like *lilybaea*); Kandavu, ♂ 1, ♀ 3. The following in the *Eastern* (Lau) group provide transitional specimens: Munia, ♂ 5, slightly transitional to *lauensis* and ♂ 5, transitional to *walkeri*; Vanua Mbalavu, ♂ 13, ♀ 4, transitional to *lauensis* and ♂ 10, ♀ 1, transitional to *walkeri*. Total ♂ 121, ♀ 38, and transitional specimens, ♂ 34, ♀ 5. The two specimens from Anuta in the Santa Cruz group have been discussed under *brunnescens* (*vide supra*).

in the combined spot in 3, so typical of the *lewinii* complex. The maximal male has, on the underside of F.W., D.4 large and shaped like an arrowhead. In the maximal female, on the underside of H.W. there is an elongated pair of submarginals in area 2, and D.2 is held between the proximal ends of these. The following is the percentage development of the three special spots in 169 ♂ specimens.

F.W.					H.W.				
D.10-11 above					Cell below				
L.	N.	S.	T.	A.	L.	N.	S.	T.	A.
86.3	13.6	—	—	—	33.1	40.8	17.7	4.1	4.1

Cell below				
L.	N.	S.	T.	A.
5.9	47.3	33.7	10.1	2.9

Here the cell of the H.W. seems to have suffered reduction, that of the F.W. has been enlarged.

DISTRIBUTION. *Friendly Isles*: "Tonga", ♂ 25, ♀ 3; Tongatabu, ♂ 126, ♀ 8; Vava'u, ♂ 35, ♀ 5; Ha'apai, ♂ 7, ♀ 6. Total ♂ 193, ♀ 22.

No. 8, *bourkei*.

This subspecies has the prominent spots in F.W. areas 2-3 not so large as in *lewinii*, the spot in 3 not extending towards the base so far posteriorly as in *lewinii*. On the H.W., submarginals in areas 1c-3 are also smaller. F.W. A.4 is only exceptionally present. The under-surface shows considerable variation; some specimens are highly suffused with white or light grey as in *lewinii* so that the anal border of the H.W. has almost a bluish appearance: others, less shaded, resemble *walkeri*.

It is appropriate here to notice Poulton's difficulty over Fruhstorfer's *aglaina* (*loc. cit.*, p. 586), described as from Samoa which is the locality for *bourkei*. Poulton points out that Fruhstorfer's figure (1910) shows a very dark form and suggests that "it may be a female of *schmeltzi*". The difficulty as to the identity of *aglaina* was solved when I fortunately found Fruhstorfer's type specimen in a corner of an obscure cabinet of his collection, now in the British Museum (Nat. Hist.). This specimen is what has been known as *whitmei maréensis* Poulton, 1927, which will be discussed in its proper place later (see Talbot, 1943, 12-13). Since, in former days, "*whitmei*" was classed with *schmeltzi* Poulton's suggestion was correct at the time it was made.

DISTRIBUTION. "Samoa", ♂ type +15, ♀ 5; Upolu (Apia), ♀ type; Tutuila, ♂ 1. Total ♂ 17, ♀ 6.

No. 9, *walkeri*.

This form is more widely distributed than those previously discussed: it seems to be a wanderer, and Poulton (*loc. cit.*, p. 587) considered that it was an earlier invader "than *eschschooltzii* which has not advanced beyond western Fiji". He described *walkeri* as having a less developed pattern with darker ground-colour on both surfaces. The chief character of the spotting of *walkeri* is elongation of the paired submarginals in H.W. areas 2-3; it is shown in various degrees by specimens of *eschschooltzii* therefore classed as transitional. The H.W. admarginals are also larger than in other forms of the *lewinii* complex. The maximal male is exceptional in showing A.8 on F.W. A female from Tahiti shows an enlarged S.2 on F.W. below; it is pear-shaped, the small proximal end distinctly different

in appearance from the bulbous distal end : this is comparable with the constitution of the larger spot in area 3. The minimal female shows dyslegnic clouding over the posterior part of F.W. D.3 on the upper surface. The discal spots on F.W. underside are not all the same in colour, often 4-6 are bluish ; the H.W. discals may all be bluish.

F.W.								H.W.			
D.10-11 above				Cell below				Cell below			
N.	S.	T.	A.	N.	S.	T.	A.	N.	S.	T.	A.
48.3	42.7	7.9	1.1	18	38.2	16.9	26.9	39.3	39.3	21.4	0

The reduction of the cell-spot on the underside of F.W. is remarkable in such a well-spotted form.

DISTRIBUTION. *Fiji* : Ono, ♂ 1 ; Matuku, ♂ 1 ; Vanua Vatu, ♂ 2 ; Kambara, ♂ 4 ; Fulanga, ♂ 1 ; Lakemba, ♂ 5, ♀ 6 ; Nairai (Naiau), ♂ 2 ; Thithia, ♂ 4, ♀ 2 ; Mango, ♀ 2 ; Munia, ♂ 1 ; Vanua Mbalavu, ♂ 1, ♀ 1 ; Naitamba, ♀ 1, transitional ; Fotuna, ♂ 4, ♀ 1. *Ellice Isles* : ♀ 1 ; Union Isle or Tokelau, ♂ 1. *Tahiti* : ♂ 50, ♀ 22 ; Eimo, ♂ 8, ♀ 6 ; Moorea, ♂ 4, ♀ 1. Total ♂ 89, ♀ 43. In Tahiti *walkeri* ranks as a subspecies, but it occurs sporadically on many islands in Fiji. Whether these occasional captures result from wandering specimens, or whether they are survivals from a former wider distribution is a difficult question.

No. 10, *perryi*.

This is the oldest name for forms with different degrees of reduction of the spots, which have from time to time been described as *intermedia* and *indistincta* Moore, 1883 and *unicolor* Druce, 1890. The maximally spotted male has the large F.W. D.3 longer than in *distincta*, but in the maximal female it is small and shows itself to be what by origin it really is, a submarginal. The maximal male has a F.W. S.4 below, which is unusual : the minimal male is the extreme "*unicolor*" in which no spots are seen above. The type *perryi* has F.W. D.3 much contracted on the upper side, though not below, by black suffusion : below the coloration is uniformly brown. This variable subspecies, *perryi*, might have been derived from *eschscholtzii* through *lauensis*.

DISTRIBUTION. Niue, ♂ 18, ♀ 3 ; Samoa ("Navigators Isle"), ♂ 1 ; *Cook Islands*, type ♂ *perryi*, Aitutaki, type ♂ "*unicolor*" +4, type ♀ "*unicolor*", Rarotonga, type ♂ "*indistincta*" +1 ♀ 2. Total ♂ 27, ♀ 6.

No. 11, *doretta*.

Male type, F.W. very dark brown, H.W. disc of same colour with paler border. F.W. submarginals bluish above and all spots on underside bluish-white on both wings. Female type lighter than male ; outer third F.W. and border H.W. paler. Spots white above. The costal spot D.10 on F.W. is only exceptionally shown as a trace on the underside of the maximal male.

DISTRIBUTION. *Admiralty Isles* : Manus (reported) ; Los Negros (reported). *Bismarck Archipelago* : New Britain, ♂ 17 ; Duke of York Island, ♂ type +1, ♀ type +1 ; New Ireland, ♂ 3 ; Queen Charlotte Island, ♂ 4 ; Feni, ♂ 6. Total ♂ 32, ♀ 2.

No. 12, *macleari*.

F.W. uniform dark brown ; H.W. paler with sharply marked white marginal band in which admarginals are lost. Discals and cell-spots below bluish.

DISTRIBUTION. *Christmas Island*, in Indian Ocean: ♂ 16, ♀ 1. *N.W. Australia*: Raebourne, ♂ 1. Also recorded from Derby, north-east of Raebourne. Total ♂ 17, ♀ 1.

No. 13, *nobilis*.

A very suitably named, smart-looking, species. The large cell-spot on F.W. is pure shining white, but S.6-7 may be bluish. Ground colour of F.W. very dark purplish-black, and disc of H.W. of the same colour but the costal area broadly white from costa to behind vein 7.

DISTRIBUTION. "*Admiralty Isles*": ♂ type +9, ♀ type +1; Manus, ♂ 4; Los Negros, ♂ 2. Total ♂ 16, ♀ 2.

No. 14, *lugens*.

This subspecies is close to the next, *misagenes*, but has the F.W. submarginals bluish above while in *misagenes* they are white. Also, in *lugens* the discals and cell-spots on the underside of both wings are bluish, in *misagenes* the blue tint only shows on the H.W., and not always so. The maximal male of *lugens* shows S.1a on underside of H.W., a very rare occurrence. The inward displacement of S.3 on the F.W., so characteristic of forms of *lewini*, is also seen in *lugens*.

DISTRIBUTION. "*British New Guinea*": ♂ type +2; Owen Stanley Mountains, ♂ 5; Mt. Alexander, ♂ 1; Port Moresby, ♂ 3. Total, ♂ 12. Strictly speaking this subspecies does not come into the definition of the area considered, for forms confined to New Guinea have not been included. But *lugens* is so close to *misagenes* that it was interesting to include it.

No. 15, *misagenes*.

The maximal female has a submarginal on the upper side of F.W. area 1a which is rare; also it has in area 1c of H.W. a short extra pair in the submarginal series interposed along the inter-neural fold.

DISTRIBUTION. Dampier Island, ♂ 6, ♀ 6.

No. 16, *weneri*.

A feature of *weneri* is the presence of discals on the upper side of F.W. in male as well as female, but not on H.W. except in maximal female. Both sexes have a discal streak on upper side of F.W. in 1b. The maximal male has D.2 and 6 on F.W. forked externally; both sexes may have D.8 on F.W. below, which is rare.

DISTRIBUTION. Vulcan Island, ♂ type +6, ♀ type +5. Total ♂ 7, ♀ 6.

No. 17, *jennessi*.

The well-developed, violet-tinted, submarginals on F.W. give both types a resemblance to *guerini violetta* Butler, 1876, but the brand is lacking and there is no general purple gloss on the uniformly dark brown F.W. Slips in description of spots in my original description (1942) are now amended. A female, found unplaced in the national collection, seems to be a variant from the type female, but agrees in general appearance. F.W. submarginals faintly violet, S.6 with a white spot externally and S.7 mostly white.

DISTRIBUTION. Goodenough Island, ♂ type, ♀ type. *New Guinea*: "Port Moresby or Yule Island", ♀ 1. Total ♂ 1, ♀ 2.

No. 18, *insulicola*.

Somewhat like *subnobilis* (No. 46) but without a brand; F.W. of the same dull purplish brown, H.W. with similar grey-brown costal area but in *insulicola* it extends rather further back. The F.W. cell-spot in *insulicola* may be bluish above. From *nobilis*, *insulicola* may be distinguished as follows:—

		<i>insulicola</i>	<i>nobilis</i>
Upper side	F.W.	Not so dark a brown, narrow streak 1b.	Almost black, no streak 1b.
	H.W.	Costa grey-brown as far back as vein 4 or 5, Submarginals 4-6 usually small.	Costa white as far back as middle of area 6, no submarginals.
Underside	F.W.	1a grey-brown, streak in 1b.	1a white, no streak in 1b.

DISTRIBUTION. "Admiralty Isles": ♂ type +3, ♀ type. Manus, ♂ 3, ♀ 10. Total ♂ 7, ♀ 13.

No. 19, *cerberus*.

The following spots are unique or very rare: male, F.W. above A.3-6, cell, F.W. below D.5; female, F.W. below D.5.

This species is very like *obscura* (No. 22) but has the F.W. slightly paler above in its outer part while in *obscura* it is more uniformly dark. The spotting on *cerberus* is more definite: on the underside there is always D.2 on F.W. which is absent from *obscura*. On the other hand, *obscura* has D.5 on F.W. which is only exceptionally present in *cerberus*, and *obscura* may have more H.W. Subs. than 4-6, but *cerberus* never has. The maximal male *cerberus* has a cell-spot and admarginals on the F.W. above, which is exceptional: also D.5 below which is present in the female. The inner margin of F.W. in *cerberus* male is more definitely curved than in *obscura*.

DISTRIBUTION. "New Guinea": ♂ 1; Astrolabe Bay, ♀ 1; Stephansort, ♂ 3, ♀ 1. *Bismarck Archipelago*: Rooke Island or Umboi, ♂ 3, ♀ 3; New Britain, ♂ type + 25, ♀ type + 9; Duke of York Island, ♂ 1, ♀ 1; New Ireland, ♂ 4; Steffanson Island, ♂ 1; Queen Charlotte Island, ♂ 1; Feni, ♂ 2, ♀ 2. (It is interesting to note that I have also seen the following from the *Schouten Islands*: Biak and Bosnick, ♂ 22, ♀ 19; Korrido, ♂ 7.) Total ♂ 71, ♀ 37. It is worth noting that *cerberus* has not found its way to the Admiralty group, although it seems plentiful on the Schouten Isles. Two males in the Rothschild collection collected by Webster bear the very unlikely data "New Georgia".

No. 20, *subpunctata*.

This little-known form is difficult to separate from *cerberus*: it presumably derives its name from the absence of spots on the upper surface. It never has F.W. D.5 below.

DISTRIBUTION. New Ireland, ♂ 2, ♀ 5. In as much as it shares New Ireland with *cerberus* they cannot be geographical races: possibly they are ecological species, or even true species.

No. 21, *griseitincta*.

A geographical derivative of *cerberus* from which it differs by the grey-brown tint toward the apex of F.W.

DISTRIBUTION. St. Mathias Island, ♂ 6, ♀ 1.

No. 22, *obscura*.

This species has been discussed with *cerberus*.

DISTRIBUTION. *Bismarck Archipelago*: New Britain, ♂ 13, ♀ 2; Duke of York Island, ♂ type +5, ♀ type; New Ireland, ♂ 1; Queen Charlotte Island, ♂ 1. Total ♂ 21, ♀ 3.

No. 23, *eboraci*.

The general ground-colour is a uniform golden brown. In the male the minute submarginals of F.W. are blue. On the underside of F.W. the spots are strongly eulegmic and shining white except in the cell which has a blue spot: on the H.W. all spots beneath are white. In *eboraci* F.W. S.3 is not displaced inwards as it is in *cerberus*.

DISTRIBUTION. *Bismarck Archipelago*: New Britain, ♂ 3, ♀ 4; Duke of York Island, ♂ type +3, ♀ type. Total ♂ 7, ♀ 5, including ♂ 1 ex Joicey collection with locality "German New Guinea" which needs confirmation.

No. 24, *melia*.

This form can scarcely be separated from the next if large numbers are seen. All that can be said is that in maximal *melia* the spots are very slightly larger than in the maximal *catana*. The spots, such as they are, are blue in the maximal female; on H.W. they become radiating streaks.

DISTRIBUTION. *D'Entrecasteaux Archipelago*: Goodenough, ♂ 17, ♀ 3; Fergusson, ♂ type +9, ♀ type +1. Total ♂ 27, ♀ 5.

No. 25, *catana*.

The maximal female has on F.W. underside a submarginal in 2 of the same yellow as the main patch. This is the only F.W. spot seen on all the specimens of *melia* and *catana*.

DISTRIBUTION. *New Guinea*: ♂ 12, ♀ 2; Wilhelmshafen, ♂ 5, ♀ 1; Finschhafen, ♂ 1; coast near Finisterre Mountains, Ekeikei district, Milne Bay and Port Moresby, ♂ 32, ♀ 7. Total ♂ 50, ♀ 10.

No. 26, *auritincta*.

Distinguished by the light golden brown ground-colour; spotless above.

DISTRIBUTION. *Bismarck Archipelago*: New Ireland, ♂ 4.

No. 27, *trobriandensis*.

Uniform dark reddish brown; male spotless above, female with minute spots. The few spots are almost round dots, not elongated as in *honestia*.

DISTRIBUTION. *Trobriand Archipelago*: Kiriwina, ♂ type +1, ♀ type; Woodlark, ♂ 2. Total ♂ 4, ♀ 1, in British Museum (Nat. Hist.).

No. 28, *nanum*.

A single small specimen, unicolorous soft purplish brown above, spotless. Below, slightly paler at margins.

DISTRIBUTION. *Trobriand Archipelago*: Woodlark, ♂ type, in British Museum (Nat. Hist.).

No. 29, *rotunda*.

This New Guinea race had to be noticed because of a specimen from the Louisiade Archipelago; it is one of several dark forms of *batesii* (e.g., *gorgonia* Hulstaert,

1924, from Dutch New Guinea and *publilia* Fruhstorfer, 1910, from former German territory) but the underside is darker.

DISTRIBUTION. *British New Guinea* (type): Hydrographer Mountains, ♂ 1, ♀ 3; Milne Bay, ♀ 1; Port Moresby, ♂ 12, ♀ 3; Moroka to Mt. Nisbet, ♂ 1; Kebea, 3,600 ft., ♂ 1; Mekeo district, ♂ 1; Yule Island, ♂ 1, ♀ 1. *Louisiade Archipelago*: Conflict Island, ♀ 1. Total ♂ 17, ♀ 9.

No. 30, *belia*.

No specimens being available the notes on spots are taken from the admirable figures given by Waterhouse (1914, figs. 10, 12). It appears to be similar to the last-named, with a paler border and in the male "very faint indications of a series of large pale outer-discal spots". Two males and two females are recorded from Cape York, Darnley Island and Murray Island. Waterhouse says "we have specimens from Orokololo, Gulf of Papua, which we consider identical with the Australian race".

No. 31, *resarta*.

The nomino-typical form has brownish white spots on a dark brown ground. The pattern is formed by well-developed submarginals on the F.W. assisted by admarginals on H.W. It is an extremely variable race, the most strongly patterned forms having the spots whitest while the darker forms may show no spots at all on F.W. upper side, and only ghosts of spots on the H.W. The darkest specimens are near to *rotunda* and occur with it at Port Moresby. Since the various named forms grade easily into one another and three of them (*resarta*, *funerea* Butler, 1878 and *squalida* Butler, 1878) all occur at Port Moresby, while *turbonia* Fruhstorfer, 1910 and *murena* Fruhstorfer, 1911, both occur on Goodenough island, it has seemed impracticable to attempt a distinction and all are included under *resarta*.

In the maximal male, F.W. S.1b is large and shaped like an arrowhead; on the H.W. there is, in 1c, an intermediate streak between the two spots: on the underside of the F.W. D.5-6 are exceptional. The maximal ♀ has the fused pairs of S.1-6 very large on F.W.; on H.W. the pairs of Ads. and Subs. are completely fused in 1b-5, but separate pairs in 6. Discal and cell-spots, especially on H.W., may be blue.

A male from the Hydrographer Mts. has F.W. Subs. small and quite discrete, H.W. Subs. unusually narrow and the Ads. mostly small and discrete. The male from Yule island is unusual in that the members of each pair of Ads. and Subs. on H.W. are joined differently from the normal; each member of a pair of Ads. is joined to its corresponding member of the pair of Subs., and the two Ads. of a pair are not joined together. A maximally spotted male has a peculiar aberration; between the members of a pair of inwardly extended Ads. on the H.W. there is a closely knit pair lying along the inter-nervular streak of 1b.

DISTRIBUTION. ex *German New Guinea*: ♂ 5, ♀ 5. *British New Guinea* (chiefly Port Moresby with ten specimens from Hydrographer Mountains): ♂ types of *funerea* and *squalida* + 36; ♀ type of *resarta* + 14; Yule Island, ♂ 5, ♀ 1. *Louisiade Archipelago*: Conflict Island, ♀ 1; Nivani, ♂ 3; St. Aignan, ♂ 1; Sudest, ♂ 3. *D'Entrecasteaux Archipelago*: Goodenough, ♂ 6, ♀ 2; Fergusson, ♂ 1. Total ♂ 62, ♀ 24.

No. 32, *kunggana*.

This new subspecies, obviously derived from *resarta*, is dark velvety black with pure white spots. The male holotype has wing-span of 76 mm., the paratype measures 73 mm. The F.W. has S.1b-9 of which 6 is the longest. The H.W. has S.1b-6; in 1b-3 the paired spots are separate, in 4-5 the pairs are fused but an external notch shows the original admarginals, now lost in the conjoint spot. There is a separate pair of Ads. in 6 of which the posterior extends inwards as a streak.

The female allotype has the ground-colour slightly browner than the male. F.W. on upper side has a single row of spots as in the male but 6 is more prolonged inwards. On H.W. the two Ads. in 6 are small, quite distinct from each other and from the Subs. Below, on F.W., the Ads. are irregular and attached to the ends of the Subs., and there is a trace of a cell-spot. The discals are well developed, and slightly blue. The H.W. is as in the male but there is a trace of the cell-spot.

DISTRIBUTION. *Solomons*: Rennell Island, Kunggana Bay, ♂ 2, ♀ 3. Collected by M. Willows, Jr., on the Templeton-Crocker expedition 1933. Male holotype, female allotype 6th June; paratypes 14th June. Types and ♀ paratype in California Academy of Sciences. ♂ ♀ paratypes in University Museum, Oxford. (See addendum (p. 157) for further specimens.)

No. 33, *honesta*.

This characteristic Solomon Island subspecies seems to fall into two groups, the discal spots of F.W. being well or poorly developed: the latter group includes Ribbe *faisina*, and the male of Strand's *bigamica* 1914; I have now found that the female "*bigamica*" belongs to No. 60, *boisduvalii fraudulenta*! The female holotype of *honesta* belongs to the well-spotted series; the cell-spot is large on each wing, and on F.W. underside has the arrow-head shape suggesting paired origin.

Some specimens have the cell-spot and streak 1b, on F.W. upper side, purple; the markings in 1b may be one or two streaks, or elongated spots, and vary much in length. F.W. D.2 may be forked at the end.

DISTRIBUTION. (A) Well-spotted forms: "*Solomons*", ♂ 7, ♀ type +4; Shortlands, ♀ 4; New Georgia (Rubiana), ♀ 1; Guadalcanal, ♂ 24, ♀ 18; Florida, ♂ 1, ♀ 1. (B) Poorly-spotted forms: Bougainville, ♂ 7, ♀ 3; Shortlands, ♂ 1; Choiseul, ♂ 3, ♀ 1; Vella Lavella, ♂ 3, ♀ 3; Kolombangara, ♂ 3, ♀ 1; New Georgia, ♂ 2; Rendova, ♂ 1; Ysabel, ♂ 10, ♀ 5; Russell Isles, ♂ 1; Florida, ♂ 4. Total, ♂ 67, ♀ 42. The complete absence of *honesta* from San Cristobal, Santa Ana and Santa Catalina has a significance to be discussed later.

No. 34, *woodfordi*.

This strikingly white subspecies seems rare. The female has the white areas more developed; in the male type the F.W. subapical area is only slightly paler where it is white in the female. The F.W. discals on the underside of the maximal female are faintly blue, and on F.W. the spot in 2 is forked externally.

DISTRIBUTION. *Solomons*: Malaita, ♂ 4, ♀ 6.

No. 35, *leucacron*.

The only known specimens of this new subspecies, both males, differ very slightly in spotting. There is a definite pure white tip to the F.W. from area 10 to area 4;

on the underside the white, in the type, extends narrowly back to vein 2; in the paratype it reaches the tornus. The H.W., beneath, has a narrow white marginal band from apex to anal angle, of uniform breadth slightly wider in the type.

DISTRIBUTION. Type and paratype, ex Rothschild collection in British Museum (Nat. Hist.). The type is labelled "San Christoval". The latter bears a written label "Australia, Leggett" which is certainly incorrect. Another written label, more recent, has "? Ugi" which is a very possible locality.

No. 36, *coffea*.

This form is considered on account of its presence on Dampier Island; it is very close to *occulta* Butler, 1877, into which it grades, and they occur together. Typical male *coffea* has a paler margin to F.W. and on H.W. a large pale anal area extending narrowly forwards to area 4. The female has the F.W. apex whitey-brown and the whole border very pale, while the anal area of H.W. is as pale as apex of F.W. The presence of admarginals on underside H.W. is exceptional. One male specimen from Dampier can only be distinguished beneath from an *occulta* by the presence of H.W. submarginals not shown in *occulta*.

DISTRIBUTION. ex *German New Guinea*, ♂ 3; Humboldt Bay, ♂ 4 (+); Dampier Island, ♂ 3; Orange River, ♂ 1; Astrolabe Bay, ♂ 11, ♀ 4 (+); Erima, ♂ 5, ♀ 8 (+); Stephansort ♂ 11, ♀ 10 (+); Constantinehaven, ♂ type +2, ♀ 3; Sattelberg, ♂ 3; Simbang, ♂ 1. Total ♂ 45, ♀ 25. The sign (+) indicates that in the same locality *occulta* occurs.

No. 37, *diadema*.

A New Guinea subspecies, *diadema* is included here because of two specimens from Goodenough Island. Moore's "male" type is actually female; its ground-colour is slightly paler than that of *macgregori* female and lighter than the deep velvety black of a male. The spots are not quite pure white. The maximal male has F.W. Subs. 2-3 in the shape of arrow-heads.

DISTRIBUTION. "New Guinea" ♂ 3, ♀ type. "British New Guinea" ♂ 1; Milne Bay, ♂ 4, ♀ 7; Astrolabe range, ♀ 1; "Mailu" (?=Maliu or Toulon Island), ♂ 2, ♀ 4; Port Moresby, ♂ neallotype +3; Owen Stanley Mountains, ♂ 1; Aroa River, ♂ 1, ♀ 5. *D'Entrecasteaux Archipelago*: Goodenough, ♀ 2. Total ♂ 16, ♀ 20.

No. 38, *macgregori*.

The ground colour of F.W. is dark purple brown but H.W. is lighter; the underside is dark chestnut brown. The F.W. Subs. are reduced as compared with *diadema* while those of H.W. are larger.

DISTRIBUTION. *D'Entrecasteaux Archipelago*: Normanby, ♂ type; Fergusson, ♂ 11, ♀ 2; Goodenough, ♂ 6. Total ♂ 18, ♀ 2. As it occurs with *diadema* on Goodenough they both rank as "forms" not geographical races.

No. 39, *samaraina*.

The holotype is the only known specimen of this striking new subspecies. Reduction of F.W. Subs. has gone further than in *macgregori* but S.6 is large and conspicuously white both above and below. The discals and cell-spots on both wings beneath are bluish. The F.W. is intense velvety brownish black above, on the H.W. underside there is a strong purple gloss.

DISTRIBUTION. Samarai Island, at east end of New Guinea, ♂ holotype. In British Museum (Nat. Hist.) ex Adams bequest.

No. 40, *monilifera*.

Very near to *diadema*. The ♀ holotype in the British Museum (Nat. Hist.) has locality Thursday Island. Miskin (1890) recorded this subspecies from Cape York as *misenus*.

No. 41, *eichhorni*.

This has a strong resemblance to *sylvester* (see Talbot, 1921); it is about the same size, which is small for a form of *alcathoe*. The strong development of admarginals and elongation of H.W. Subs. helps the resemblance, which is particularly noticeable on the underside. The Subs. of F.W. are small and very close to the Ads.

DISTRIBUTION. Musgrave (1948) says that *eichhorni* ranges from Herbert River to Cape York.

The specimens I have examined are from the following localities. "North Australia", ♂ 3, ♀ 2.

Queensland (Kuranda, Cooktown, Wright's Creek), ♂ 5, ♀ 2; Cairns, ♂ 4. No data, ♂ 4, ♀ 1.

Total ♂ 16, ♀ 5.

No. 42, *lacon*.

The F.W. has dark purple gloss, and the spots above are blue; the H.W. spots are white. The dark brown costa of H.W. distinguishes *lacon* from *nobilis*.

DISTRIBUTION. Bismarck Archipelago: New Britain, ♂ type +3, ♀ type +1; Duke of York Island, ♂ 1. Total ♂ 5, ♀ 2.

No. 43, *corinna*.

A fully spotted species. On F.W. underside the discal and submarginal in 3 do not merge, as in *lewini* forms. S.2 may be elongated into an oval. The maximal female has a F.W. cell-spot above, which is exceptional; its arrow-head shape indicates paired origin. The same female also has a tiny streak on F.W. underside in D.12 which is exceptional for any *Euploea* in this study. There may be a white streak at the base of H.W. 1b below in addition to the usual pair of submarginals.

DISTRIBUTION. Waterhouse & Lyell (1914) write "This is our most abundant Australian species, and is the only Euploeid that reaches as far south as Sydney. In the extreme north it is very variable and aberrant examples have been described by Miskin as *E. euclus*. . . his types are in the Queensland Museum". The figures given by Waterhouse & Lyell do not show so great a reduction of spots as is recorded for the minima in the tables, except that the male *euclus* lacks admarginals on H.W. upper surface, while the minimal example shows them faintly.

The fact that *corinna* is found on the north coast of Western Australia is of importance in relation to the presence on Kisser Island of a *Euploea* which I cannot distinguish from *corinna*. There are ♂ 7, ♀ 2 of this in the Rothschild collection of the British Museum (Nat. Hist.). Moreover, the species described by Kalis, 1933, as *coerti* from Bali is apparently the same as *corinna*: there is one male in the Oxford collection.

I have examined the following specimens of *corinna*:—"Australia", ♂ 2, ♀ 3; Thursday Island, ♂ 3, ♀ 4; "Queensland", ♂ 11, ♀ 5; "North Queensland", ♀ 1; Cape York, ♂ 5, ♀ 3; Lizard Island, ♂ 1; Cairns and Kuranda, ♂ 6, ♀ 9; Townsville, ♂ 3, ♀ 1; Magnetic Island, ♂ 2; Mackay, ♀ 1; Rockhampton, ♂ 1; Capricorn Island, ♂ 1; Brisbane, ♂ 21, ♀ 10; Toowoomba, ♀ 5; Bowen (Port Denison), ♂ 1, ♀ 1; "New South Wales", ♂ 2, ♀ 2; Auburn, ♂ 3; Sydney, ♂ 2, ♀ 2; "South Australia", ♂ 1; West Australia: Brock's Creek, ♂ 1; Derby District, ♂ 2; Dawson District, ♂ 1; Geraldton, ♂ 1; "North-West Australia", ♂ 3, ♀ 7; Admiralty Gulf, Cassini Island, ♂ 1; Baudin Island, ♂ 1; Champion Bay, ♂ 1; "North Australia", ♂ 1, ♀ 2; Darwin,

♂ 20, ♀ 13; Adelaide River, ♂ 1, ♀ 1; Roper River, ♂ 2; "Northern Territory", Melville Island, ♂ 1. In addition there is a series of ♂ 59 and ♀ 26 in the Rothschild collection bearing the unfortunately incomplete data on an old M.S. label "Eureka, Northern Territory, South Australia"; I have been unable to trace this locality. Total ♂ 168, ♀ 98.

No. 44, *rennellsensis*.

This new species, of very distinct appearance, is remarkably stable, and seems to be long established; the female is unknown. The ground-colour is deep blackish brown; on each wing there is a single row of spots near the margin on the H.W. resulting from complete fusion of Ads. with Subs. It is of medium size. The brand on F.W. does not extend towards the base as far as the level of the root of vein 2. The discal spot in area 2 on underside of F.W. may be a small oval or an oblique short streak thickened proximally, as in the holotype. Cell-spots are only represented by a trace on the underside of both wings in the maximal specimen. Of the submarginal spots on F.W., 6 as usual is the largest; on H.W. the Ads. and Subs. fuse together as far as area 5, in 6 the single admarginal is not united to the small submarginal.

DISTRIBUTION. *Solomons*: Rennell Island, Kungana Bay, ♂ 26. Collected by M. Willows, Jr. for the Templeton-Crocker Expedition, 1933. Holotype and paratypes in the California Academy of Sciences: other paratypes in the British Museum (Nat. Hist.) and the Hope Department of Entomology, University Museum, Oxford. (See addendum (p. 157) for further specimens.)

No. 45, *umboina*.

This single small female specimen proved very difficult to identify; it seems nearest to *charox* Kirsch, 1877, from which it differs by a slightly redder brown colour; the under-surface is of a greyer brown very close to that of *charox*. The margin of F.W. is slightly paler in the tornal area; on H.W. beyond the end of the cell there is a paler marginal band. The discal spots on F.W. and two submarginals on H.W. upper surface have not been seen in any of the five females of *charox* which have been examined. The F.W. spots above are slightly blued: all spots below are white. The specimen, in the national collection, was taken in the Bismarck Archipelago, on Rook Island or Umboi, by A. S. Meek, July-August, 1913. Seeing that all the sixteen specimens of the nearest ally of *umboina*, viz. *charox*, come from the Schouten Islands in Geelvink Bay, further specimens of *umboina* would be of interest; the one specimen may be abnormal.

No. 46, *subnobilis*.

This little-known species is dark brown with slight purple tint but not the gloss of *nobilis*. There is a conspicuous short brand; the costal margin of H.W. is not white as in *nobilis* but silvery brown or greyish. The F.W. spots of the male are mostly faint and dyslegnic, but the unique female has a conspicuously shining white D.3, and on the underside all spots are eulegmic and pearly white.

DISTRIBUTION. "Admiralty Isles", ♂ 2; Manus, ♂ type, ♀ ne-allotype. Total ♂ 3, ♀ 1.

No. 47, *illudens*.

I consider *decipiens* Butler, 1882, and *lygdamis* Fruhstorfer, 1910, to be synonyms, the former are less well spotted, the latter more strongly spotted, than normal

illudens. In both sexes the cell-spot on H.W. underside may be the largest spot on the wing. The presence of D.3 on both surfaces of F.W. of the maximal female is exceptional; F.W. D.10 is only shown in *illudens* as an exceptional trace on the underside of the maximal female.

DISTRIBUTION. *Bismarck Archipelago*: Rook Island or Umboi, ♂ 6, ♀ 1; New Britain, ♂ 41, ♀ 21 + ♂ 2 from "Kinnigunang"; Duke of York Island, ♂ type of "*decipiens*" + 16, ♀ types *illudens* and "*decipiens*" + 7; New Ireland, ♂ type *illudens* + 23, ♀ 4; Queen Charlotte Island, ♂ 8, ♀ 3; Squally Island or Emirau, ♂ 1; Feni, ♂ 5, ♀ 2; Nissan, ♂ 4, ♀ 12. Total ♂ 106, ♀ 54.

No. 48, *mathiasana*.

Described from specimens slightly smaller than *illudens*, with a greyer tint towards F.W. apex; the spots more noticeable than in *illudens*.

DISTRIBUTION. *Bismarck Archipelago*: St. Mathias Island, ♂ 15, ♀ 5. It is interesting that on the not very distant Nissan Island the specimens of *illudens* are of the *nomino*-typical form.

No. 49, *amycus*.

No specimens being available the notes in the table are from figures by Waterhouse & Lyell (1914). They record, from Thursday and Darnley Islands, ♂ 7, ♀ 3; the males showing considerable variation.

No. 50, *reginae*.

The locality, Queen's Islands, where J. J. Walker captured this interesting new subspecies, is mentioned by him in 1891, *Entomologist's Monthly Magazine*, **27**, 236; it lies in Admiralty Gulf of the north-west coast of Australia at about the meeting point of 125° E. and 15° N.

Reginae is as large as *eleutheria* Fruhstorfer, 1910, from Teon, *i.e.*, larger than *sacerdos* Butler, 1883, but paler brown. Compared with *eleutheria* the members of the pairs of submarginals in H.W. 2-3 are not so well fused together and the spots on both wings are smaller, especially S.3 on F.W. which is not so prolonged inwards as in *eleutheria* and does not meet D.3. The female has the cell-spot and D.2-3 of F.W. below, and all the discals and cell-spot of H.W. below, slightly blued; they are white in the male.

DISTRIBUTION. *N. W. Australia*: Queen's Island, ♂ type, ♀ allotype; Thursday Island, ♂ paratype. Total ♂ 2, ♀ 1, in British Museum (Nat. Hist.).

No. 51, *irene*.

The brand may be so short as only to occupy the middle third of F.W. 2; the costal area of H.W. is silvery. On the underside of both wings, beyond the discal spots, there is a slightly paler brown band. F.W. D.10 is present in all three males from Fergusson but lacking in some from Kiriwina. The spots are better developed in Fergusson specimens, and these have a paler tornal area below. The Egum specimen has a paler submarginal band on both wings above; D.10 is present, and the brand larger.

DISTRIBUTION. *Trobriand Archipelago*: Kiriwina, ♂ type + 7, ♀ type + 2; Egum (Yanarba), ♂ 1. *D'Entrecasteaux Archipelago*: Fergusson, ♂ 3, ♀ 1. Total ♂ 12, ♀ 4.

No. 52, *eleutho*.

Specimens from Saypan are slightly smaller than those from Guam. The presence of A.4 on upper side of male F.W., and D.8 on underside of maximal female H.W. below is exceptional.

DISTRIBUTION. *Marianne Islands*: Guam, ♂ 100, ♀ 7; Saypan, ♂ 10, ♀ 4. Total ♂ 110, ♀ 11.

It is of interest to quote here from a record by Gibson-Hill (1947) of the occurrence of *eleutho* on Christmas Island in the Indian Ocean, as a subspecies "first taken on Christmas Island by Mr. M. W. F. Tweedie who caught a single male at the end of August, 1932. Several other specimens were seen . . . It has a strong flight, seldom settling . . . Numbers were seen from July to September in 1939 and from June to August in 1940, and two males . . . were taken in July and August of the former year. These males agree very closely in wing pattern with Mr. Tweedie's specimen".

No. 53, *abjecta*.

This remarkably isolated species has most of the spots elongated or pear-shaped. Submarginals are surrounded by darker shading which, in F.W. area 5, alone shows the position of the absent spot in the type. On the underside of H.W. there may be minute blue streaks, and there may be a blue cell-spot.

DISTRIBUTION. Palau or Pelew, ♂ 22, ♀ 7; Philippine Isles, ♂ 5. Total ♂ 27, ♀ 7.

No. 54, *helcita*.

Formerly known as *whitmei* Butler, 1877, a form of *schmeltzi* H-S, 1869 (see Talbot, 1943, p. 13). F.W. area 4 has neither admarginal or submarginal spots.

DISTRIBUTION. *New Caledonia*, ♂ 4. *Loyalty Isles*, ♂ 2; Lifu, ♂ 28, ♀ 13; Uvea, ♂ 1. Total ♂ 35, ♀ 13. Also reported by Viette (1950) from Île des Pins.

No. 55, *aglaina*.

There has been great confusion over this form which Fruhstorfer in 1910 described. The figure seems slightly incorrect as it gives a row of three spots at apex of H.W. of which the precise localization is obscure. Reference has been made previously (p. 83) to the difficulty in understanding the description although, in fact, the figure, with the exception mentioned, gives a good representation of the type. Fruhstorfer's *aglaina* is the same as Poulton's *maréensis* which sinks as a synonym. Unfortunately, this does not clear up all the inaccuracies. The type of *aglaina* is labelled as from "Mahé", a quite impossible locality, in the Seychelles. By a curious coincidence the ♂ type and ♀ allotype of Poulton's *maréensis* from the Loyalty Isles have the locality written "Mahé", as Poulton noted (1927, p. 50). The catalogue of Fruhstorfer's types, in the British Museum, gives the locality for *aglaina* as "Nahé".

DISTRIBUTION. *Loyalty Isles*, ♂ 1, ♀ 2.

No. 56, *schmeltzi*.

The maximal male has several exceptional spots, *e.g.*, F.W. S.4 on both surfaces and cell-spots below, H.W. D.7 below. F.W. S.3 is paired, and arrowhead shaped. The maximal female has a broad whitish margin on underside H.W. embracing both Ads. and Subs.

DISTRIBUTION. "*Samoa*", ♂ 23, ♀ 14; Upolu, ♂ 80, ♀ 33, Savai, ♂ 24, ♀ 3; Monono, ♂ 1, ♀ 1. Total, ♂ 128, ♀ 51. The absence from Tutuila is striking.

No. 57, *nechos*.

This is noteworthy for the very large brand, which in the antero-posterior dimension exceeds that of any other form mentioned in this study. Spots on the upper side are only shown in the female. On F.W. underside D.2 makes a conspicuous bar, and in the male others may be blue, as they are on H.W. The maximal female has, on F.W. below, conspicuous white suffusion between D.2-3 and 3-4. Some specimens show a distinct paleness of the margins which, in *prusias* (*vide infra*), has been exaggerated into a white border.

DISTRIBUTION. "*Solomon Islands*", ♂ 2; Bougainville, ♂ 8, ♀ 4; Shortlands, ♂ 16; Treasury, ♂ type; Choiseul, ♂ 3, ♀ 4; Vella Lavella, ♂ 9; Gizo, ♂ 1, ♀ 2; Kolombangara, ♀ 3; New Georgia, ♂ 1, ♀ 1; Rubiana, ♂ 1, ♀ 1; Ysabel, ♀ 3; Huleo, ♂ 7; Florida, ♂ 5, ♀ 5; Nangatana, ♂ 3; Tulagi, ♂ 15, ♀ 1; Guadalcanal, ♂ 26, ♀ 2 + Aola, ♂ 10, ♀ 2. Total ♂ 108, ♀ 28. No specimens have been seen from Fauro, Ganongga, Rendova or Russell Isles. The significance of the absence from Malaita, and from San Cristobal with its small neighbours, is discussed below. A male which was kindly sent me from Leiden museum bore data "♂ New Guinea. Staud.". This locality is unique and needs confirmation: possibly it should have been Bougainville.

No. 58, *prusias*.

This is spotless above, with a broad white border.

DISTRIBUTION. *Solomon Islands* (those lacking *nechos*). Ulawa, ♂ type + 1; Ugi, ♀ 4; San Cristobal, ♂ 4; Santa Ana, ♂ 33; Santa Catalina, ♂ 1. Total ♂ 40, ♀ 4. A specimen in the national collection bears data "Aola, Guadalcanal, Woodford", but there is probably an error in the labelling.

No. 59, *pronax*.

The white border is less developed on this subspecies in the male. The male type shows only a faint paler margin of area 2 on F.W., and on H.W. areas 1b-3 are whitish near the margin with brown edging. Area 4 has a narrow whitish strip just extending across vein 5. The light-brown female allotype has the borders of F.W. 1a-1b almost white, 2-3 are brown with faint white suffusion, from area 4 and round the apex the wing is white, narrowly bordered with brown; the break in continuity of the white border of F.W. contrasts with continuous white in *prusias*; on H.W. the white extends from apex to anal margin and is broader than in *prusias*.

Some of the males only differ from *nechos nechos* by faint paling at the apex of F.W. which, moreover, is never as white as in *prusias*. Also, in some, the H.W. shows an ill-defined white area on each side of veins 1, 2 and 3, the narrow side of each area contiguous with the next; these may be developed into a continuous white band reaching forward to vein 5.

DISTRIBUTION. *Solomon Isles*: Malaita, ♂ type + 10, ♀ type. Total ♂ 11, ♀ 1. Also ♂ 1 from "Guadalcanal" which (as for the last form) requires confirmation.

No. 60, *fraudulenta*.

An extremely common and widespread species under which I include forms given undeserved names. Fruhstorfer's female *lystra* is a small specimen, slightly paler posteriorly than most, and poorly spotted above though well spotted below. His male type of *rendovana* has a second brand in 1b smaller than the normal one in front of it; three other specimens from Rendova, however, do not have

this abnormality, and three from Ulaua do possess the accessory brand. Strand's "*bigamica*" (1914) is a composite, of which the male is *honesta* as I showed in 1942 (p. 128) while the female I have now discovered is a *fraudulenta*. Lastly, there is the mythical "*vitella*" of Montrouzier, 1856, which, from the inadequacy of the description has baffled identification, the type being non-existent. I applied to Paris, and Monsieur J. Bourgogne did his best for me without success. But a clue can be found in the original description which mentions "Dessous des supérieures marqué sur le limbe de trois points et d'un trait bifide blancs . . .". This fits well with many specimens of *fraudulenta* (see Pl. 2, fig. 5); on the underside of F.W. D.2 is large and very often has a bifurcated extremity. Montrouzier's locality, Woodlark, is also in accordance with the distribution of *fraudulenta*. I therefore conclude that "*vitella*" is probably what is now known as *fraudulenta*. There is much variation in the size of *fraudulenta*; specimens from the eastern parts are often smaller, and it grades into smaller forms on the islands to south and east. Spotting varies in degree even on one island; maximal development is found on Faisi, Ganongga, Ysabel, and Guadalcanal; minimal development on Shortlands, Ganongga, Nangatana, Undeka, Ulaua, and Guadalcanal. The enlargement of D.2 on underside of F.W. into a bar (which may be forked externally as in "*vitella*") distinguishes *fraudulenta* from a specimen of *herrichii* (No. 70) unspotted above like *fraudulenta*; the brand in *herrichii* is smaller. Generally, on the underside, admarginals are very little developed on F.W. except in the maximal female, and only exceptionally occur in the anal area of H.W. The following spots have been noted as exceptional: male underside, F.W. A. pairs 2-7, D. 5-6 and 9-10; H.W. S.1c, trace 7. Female, upper side F.W. S.8, D.10; H.W. A.6, S.6. Underside F.W. S.1b, D.9.

The maximal female may show on underside of F.W. an accessory streak along vein 4 and there may be an accessory to the H.W. cell-spot. In the minimal female F.W. D.2 is reduced to an oval spot, foreshadowing its small size in the smaller forms to the south east.

DISTRIBUTION. *New Guinea*, ♂ 1 (ex Fruhstorfer collection, doubtful). *Trobriland Archipelago*: Woodlark, ♂ 15, ♀ 4. "*Solomons*", ♂ type +1, ♀ type +1; Bougainville, ♂ 18, ♀ 16; Treasury, ♂ 3, ♀ 1; Shortlands (including Alu), ♂ 26, ♀ 6; Faisi, ♂ 2; Lofung, ♂ 9; Kamaliai, ♂ 7; Ovau, ♂ 3; Fauro, ♂ 10, ♀ 3; Kundikaboko, ♂ 13; Choiseul, ♂ 6, ♀ 1; Vella Lavella, ♂ 42, ♀ 9; Ganongga, ♂ 9, ♀ 1; Gizo, ♂ 5, ♀ 2; Narovo, ♂ 1; Kolombangara, ♂ 50, ♀ 6; New Georgia, ♂ 3, ♀ 2; Rubiana, ♂ 2, ♀ 3; Rendova, ♂ 15, ♀ 3; Ysabel, ♂ 20, ♀ 6; Islets near Ysabel, ♂ 4; Russell Isles, Yandina, ♂ 2; Lingatu, ♂ 5; Savo, ♂ 6, ♀ 1; Nangatana, ♂ 1; Undeka, ♂ 1; Florida (with Tulagi), ♂ 54, ♀ 19, and ♀ 1 trans. to *pyrgion*; Guadalcanal, ♂ 112, ♀ 30; Ulawa, ♂ 8; Rennell, ♂ 2. *Santa Cruz*: Utupua, ♂ 1. *Torres Isles*: ♂ 4, ♀ 2. Total ♂ 461, ♀ 127, plus 1 trans. to *pyrgion*. While *fraudulenta* extends from Woodlark and Bougainville to Utupua and the Torres Isles there are notable exceptions in the Solomons. None have been recorded from Malaita, San Cristobal, or its small neighbours. Through the kindness of the Director, South Australian Museum, I have seen one *fraudulenta* from the unusual habitat Ugi. Enquiry elicited that the specimen had been collected by the Rev. R. T. Mathews and labelled by A. M. Lea who was "meticulously careful". Notwithstanding, the locality must be viewed with suspicion pending confirmation by other specimens. There is a complete parallel with *nechos*, for the islands lacking *fraudulenta* are, as with *nechos*, those on which white-bordered forms prevail. The occurrence of *fraudulenta* on the Torres Isles, collected by that very careful naturalist J. J. Walker in 1900, is of interest because from those islands a specimen has been examined which suggests interbreeding between *fraudulenta* and the form *torvina*, of the New Hebrides. It is a small

male but has a large brand: the F.W. shows a paler marginal area as in *torvina*; on the underside it has a minute S.3, a slightly elongated D.2, and D.3-4. The H.W. has A. prs. 4-5, single 6 (*torvina* never has admarginals), S.5-6, D.1c-7 and cell. A specimen from Guadalcanal, small and poorly spotted, is very near *torvina*, and so is the male from Utupua in Santa Cruz. Some *fraudulenta*, from islands other than Malaita, are paler towards the margins of the wings, foreshadowing the next form, *pyrgion*.

The nearest approach to *fraudulenta*, to the west, seems to be *algea* Godart, 1819 (see Talbot, 1943, p. 14) under which name *duponcheli* Boisduval, 1832, *anthracina* Butler, 1866, and *lykoatis* Fruhstorfer, 1910 have been placed as synonyms. The brand in *algea* however is narrower antero-posteriorly and somewhat more curved transversely.

The large size of F.W. D.2 on the underside of *fraudulenta* may be correlated (? synaposematically) with its similar large size in *nechos*, for beyond the range of *nechos* to the south east it is interesting to see how the size of D.2 shrinks in the small forms until it is only an ordinary spot, and in the Eastern Fijian *mangoensis* (No. 72) also D.2 is not enlarged. The same feature distinguishes *algea*, also beyond the range of *nechos*, to the west: this subspecies can be differentiated from *fraudulenta* by the constant presence of D.10 on F.W. below, and of S.4-6 on the H.W.: both very inconstant in *fraudulenta*.

No. 61, *pyrgion*.

The white-bordered analogue of *nechos*, forms *pronax* and *prusias*. In the male holotype the white of the anal region does not extend forwards beyond vein 4; it obscures the spots in area 2. In the female allotype all Ads. and Subs. are thus obscured. The presence of F.W. D.10 below in male and female maximal specimens, and of D.9 in the male, and D.6 in the female, is exceptional. The shape of F.W. D.2 below varies from a short oval to a long bar, bifid externally, and joining the submarginal.

DISTRIBUTION. *Solomon Islands*: Malaita, ♂ type + 28, ♀ type + 30; Maramasike ♂ 5; Guadalcanal (Lunga), ♂ 1; Florida, ♂ 1, ♀ 2. Total ♂ 36, ♀ 33.

No. 62, *brenchleyi*.

Formerly considered a distinct species its status is, I think, uncertain (*vide* next entry); it has been placed by Corbet under *boisduvalii*. It is smaller than *pyrgion*, with broad white border, without spots above. On the underside F.W. D.2 is not elongated.

DISTRIBUTION. "*Solomons*", ♂ type + 1, ♀ type; Bougainville (Harawa), ♂ 5; San Cristobal, ♂ 38, ♀ 10; Santa Ana, ♂ 50, ♀ 2; Ugi, ♂ 10, ♀ 2; Rennell, ♂ 1. *Santa Cruz*, ♀ 1. Total ♂ 106, ♀ 16.

No. 63, *albomarginata*.

This is the first of the small forms of *boisduvalii* to be met to the south east, and the white seems to be an accentuation of the pale submarginal area seen in these, especially the female. On the F.W. the submarginal area is pure white with a narrow brown edging of 1-2 mm. width; on the H.W. the pale area is not so pure a white, though still paler than in other small forms. The white on the underside extends to the margin (except for a slight bordering of brown at the extreme apex of F.W.) and on H.W. is more sharply delimited than on the upper surface. The two females are much alike, they are in the Rothschild collection in the British Museum (Nat. Hist.); the male allotype is in the American Museum of Natural History.

DISTRIBUTION. *Solomon Islands* : San Cristobal, ♀ type, ♂ allotype ; Santa Ana ♀ paratype. Total ♂ 1, ♀ 2. This form occurs with *brenchleyi* which suggests that the latter is a separate species. On the other hand, *albomarginata* is so obviously a modification of the smaller forms of *boisduvalii* that it may be a recent production, so that we may have here an example of one subspecies (*brenchleyi*) being distinct enough as a result of long isolation to function as a species when a chance invader intrudes.

No. 64, *era*.

This subspecies, as compared with No. 66, *torvina*, is of a redder shade of brown, with less purple tint in it ; this shows especially on F.W. underside. The apex of the F.W. is not paler and D.2 is short ; on H.W. D.7 is never present. The shape of the F.W. seems broader antero-posteriorly in proportion to length of wing than it is in *torvina*.

DISTRIBUTION. *Santa Cruz*, ♂ 19. *Banks Islands* : Reef Island, ♂ 7. Total ♂ 26.

No. 65, *lapeyrousei*.

The introduction of this name into the South Pacific will surprise many. Having occasion to check the name "*paykullei*" in literature, however, I came up against a most complicated tangle of mistakes which with the very kind aid of Mr. W. H. T. Tams has now been unravelled. Boisduval, 1832, gave the following description : "7. E. de Lapeyrouse, *Lapeyrousei*. Boisd. *Alis fuscis immaculatis ad extimum pallidioribus ; anticis subtus punctis quatuor discoidalibus violaceis, posticis subtus punctis sex discoideis*. Ailes d'un brun noir, sans taches, plus pâles à l'extrémité ; dessous des supérieures, avec quatre points discoidaux violâtres ; dessous des inférieures, avec six. Très-voisine de *Melina*, dont elle n'est peut être qu'une variété locale. Vanikoro."

The type is a ♀ and bears labels that it was seen by Moore in 1881 ; it came to the British Museum (Nat. Hist.) in the Oberthür collection. This specimen has nothing to do with the species at present commonly known as "*lapeyrousei*" which belongs to another complex (*algea*). The true *lapeyrousei* belongs to the *boisduvalii* complex, of which there are other forms (Nos. 64, 66, 67, 68) somewhat similar, in the Santa Cruz and New Hebrides Islands ; the first described as No. 67 (*torvina*).

Doubleday, 1847, gives "27. *Eup. Lapeyrousei* Boisd. Fauna de l'Océanie, 97 (1832). Bourou". To him must be apportioned the blame for the subsequent confusion, caused by his apparent transfer of the locality Bourou from the last line of Boisduval's description of "*Duponchelii*" immediately preceding that of *Lapeyrousei* (i.e., "Elle se trouve à Bourou").

Butler, 1866, refers to Boisduval and Doubleday, but makes new confusion by "*Hab. Bouru (Bdv.) ; Aneiteum*". This inclusion of Aneiteum is probably due to confusion of Boisduval's female type with the somewhat similar *torvina* from Aneiteum (*vide supra*) which Butler himself described later.

Butler, 1874, cites "23. *Euploea lapeyrousei*, Boisduval, Voy. de l'Astrolabe, p. 97, n. 7. (1832)" and adds "Aneiteum (Macgillivray)". He goes on "It is just possible that this may not be Boisduval's species, as the type was said to come from Bouru ; the present species was also labelled *E. paykullei* in Mr. Saunder's collection". This new name is discussed later.

Butler, 1875, gives "No. 5. *Euploea Lapeyrousei* ♂ Boisduval. Havannah, Vaté, or Sandwich Island, 30 April, 1875. Mota Island, New Hebrides, 5th May, 1875". I have seen the Mota specimen, which is *bakeri* Poulton, 1927, the common New Hebrides race of *boisduvalii*. This was, for that date, an approximately correct association of a male with Boisduval's female. The new "species" *torvina* is then described.

Butler, 1876, has the following cryptic passage which must be quoted in full: "4. *Euploea Lapeyrousei*, *Euploea Lapeyrousei*, Boisduval, Voy. Astr. Lép. p. 97 (1832): *Euploea Batesii*, Felder, Reise der Nov. Lep., ii, p. 331 (1867). Two females. *E. Lapeyrousei* was not previously in the Museum; the small species hitherto representing it in the collection proves to be quite distinct; it is of the form and size of *E. sepulchralis*, with the coloration of the *E.-melina* group. It may take the name proposed for it by Dr. Boisduval, *E. Paykullei*."

Again, a new name, *sepulchralis* is introduced; it was founded by Butler in 1866 and refers to a member of the *climena* group, far removed from the forms hitherto discussed. The "*melina*" mentioned by Butler is not the form described by Godart, 1819 (which is in the group of *sylvester*) but the *melina* of Moore, 1857, which has been sunk as a synonym of *sepulchralis*.

The specimen mentioned by Butler could not possibly have come, as the label indicates, from "Vanikoro"; indeed, a note on the label in the same writing says "Kirby la dit de Bouru", which is more probable, although Java is the type locality and most specimens of *sepulchralis* come from there. A male of this *sepulchralis* was in the Oberthür collection, labelled "*Euploea Lapeyrousei* Bdv. Vanikoro. provenances diverses. Kirby la dit de Bourou. le ♂ no. 1 rassemble au dessous a la ♀ sauf qu'on voit chez lui quelques points subterminaux secondes ailes". There are admarginals and submarginals in H.W. 4.5.6. below. What the writer of the note had not observed was the intra-cellular spot seen on the upper surface of the F.W. which alone shows that this male has nothing to do with the true *lapeyrousei*.

Butler's reference to the name *paykullei* "proposed by Dr. Boisduval" is a mystery. Mr. Tams informs me that he has been unable to trace any proposal of this kind, either in print or among Boisduval's manuscripts. Butler used the name in 1874 (*vide supra*) and it was generally accredited to him with date 1876. However, Poulton (1924) showed it to be a synonym of *torvina* 1875. There is no evidence that Butler ever saw, what in fact exists, a male *melina* from Boisduval's collection bearing a label "*paykullii* Bd'" [sic!] but another label states that Moore saw it in 1881, and Tams concludes that either Moore told Butler about it, or Butler saw Moore's notes.

One of the "Two females" mentioned by Butler was brought to light by Tams and proved to be the form *batesii* now known as *rotunda* van Eecke, 1915, from British New Guinea. This has nothing to do with the species at present masquerading as "*lapeyrousei*" which is distinguished by the long brand. The next note shows that Butler was in confusion over this; and indeed, in the extract now being discussed he showed this by his description of the species next before "*lapeyrousei*" as *resarta*, "a very distinct species, allied to *E. lapeyrousei* . . ."; *resarta* is another form of the *batesii* complex.

Butler, 1879, now cites a male from Port Moresby in British New Guinea calling it "*Crastia Lapeyrousei* Boisduval. ♂, Port Moresby. *Eupl. batesii* of Felder, from Gilolo, seems closely allied to this".

Oberthür, 1880, discusses a male "*Lapeyrousei*" from New Guinea and another from Yule Island. "Plus grands que les individus typiques de ma collection, mais autrement tout à fait semblable. Pour cette espèce encore, la description de l'Astrolabe est tellement concise et incomplète que sans les individus typiques eux-mêmes, il serait impossible le déterminer avec quelque certitude."

These males were possibly the same form of *batesii* as mentioned above: this is certainly larger than the so-called "*lapeyrousei*".

Moore, 1883 wrote: "6. *Chirosa lapeyrousei*, Boisduval, Voy. Astrolabe, Lép. p. 97, ♂ (? 1832). Hab. Bouru (*Boisd.*). In coll. C. Oberthür. The type specimen of this species is much like *C. pierreti*, excepting that the sericeous streak is narrower and longer. On the underside the discal spots are slightly larger." *C. pierreti* is presumably the "*pierretii*" which Bryk (1937) places as a form of *netscheri* Snellen, 1889. The "sericeous streak" is indeed narrower than that of the males which are the true *lapeyrousei*. The specimen mentioned by Moore has become accepted as the male allotype of *lapeyrousei*; it was presumably associated with Boisduval's type, erroneously, by Oberthür.

Snellen (1889) discussing Lepidoptera of New Guinea, alludes to Boisduval's very superficial description, and the relation of "*lapeyrousei*" to *netscheri* which he thinks belongs to a separate group.

de Nicéville, 1898, writes of *Euploea (Chirosa) lapeyrousei* Boisduval, as follows: "Described from Vanikoro by Boisduval, recorded from Buru by Moore, who has examined the type specimen in M. Charles Oberthür's collection."

Fruhstorfer, 1910, merely refers to Moore and Oberthür.

Talbot, 1943, p. 12, writes: "*Euploea lapeyrousei* Boisduval (1832).—This was stated by the author to come from Java, Borneo, Sumatra, Amboina, Buru and New Guinea. The types agree with the subspecies of *algea* (Godt.) from northern Dutch New Guinea." The source of the information by Boisduval is not given: it is unknown to me. Talbot did not notice the disparity between the female type and the so-called male type. Later, on p. 15, he writes re "*melanopa* Röber (1887), Sekar, Dutch N.-W. New Guinea.—A careful comparison of the figure given by Röber (*Iris* 1; pl. 8, fig. 2) with a series of *lapeyrousei* Boisduval shows that these insects are identical. The latter form is confined to Dutch New Guinea. A specimen from Maccluer Gulf agrees very well with Röber's figure". Talbot's next remark concerns "*netscheri* Snellen (1889, New Guinea).—This is the oldest name for the species called *melanopa* by Corbet (1942, 267). The type locality is certainly Dutch New Guinea, probably Dorey". On p. 7 Talbot writes: "The name *netscheri* Snellen must be substituted for "*melanopa*". This therefore becomes the name of the male specimen from the Oberthür collection which has for so long masqueraded as the male (allo-) type of Boisduval's *lapeyrousei*, the type of which is a female: the types are in the British Museum (Nat. Hist.).

DISTRIBUTION. *Santa Cruz*: Vanikoro, ♂ ne-allotype + 2, ♀ type + 21; Utupua, ♀ 2. Total ♂ 3, ♀ 24.

No. 66, *matemae*.

The males are small, like those of *torvina* (*vide infra*); very dark blackish brown with a very slightly paler apex and outer margin of F.W.; on H.W. a definite broad paler margin. This subspecies is intermediate in the male between *lapeyrousei* in which there is no paler area on F.W. and *bakeri* (*vide infra*) in which there is a markedly pale area; it differs from *torvina* by absence of submarginals, and poorly developed admarginals on H.W. beneath; only in one specimen are very small A.5-6 shown. The female is like that of *bakeri*.

Only in the maximal male is F.W. D.2 extended towards the submarginal region; in the other males and the two females it is a small oval spot.

DISTRIBUTION. *Santa Cruz Isles*: Matema, ♂ type +2, ♀ 1; Anuta or Cherry Isle, ♀ 1. Total ♂ 3, ♀ 2.

No. 67, *torvina*.

This subspecies differs from *era* not only by the ground-colour but by having Ads. and Subs. better shown on H.W. underside. The female (= *paykullei* Butler, 1876) is scarcely separable from No. 68, *bakeri*; its margins are distinctly paler than in the male, which is darker brown. F.W. D.2 below is usually elongated so that in the maximal male it reaches the position of a submarginal. H.W. D.7 is present in the maximal male and female.

DISTRIBUTION. "*New Hebrides*", ♂ 1, ♀ 1. *Southern New Hebrides*: Tana, ♂ 11, ♀ 1; Aneityum, ♂ type, ♀ type +1; Malekula (Mallicolo), ♂ 1 (a very doubtful locality). Total ♂ 14, ♀ 4.

No. 68, *bakeri*.

Readily recognizable by the well-marked pale submarginal area of each wing. On F.W. in the male D.2 is variable; round, oval, or elongated bar, but in the female it is never elongated. Admarginals are only shown on H.W. in maximally spotted specimens, the discals are well developed and 7 may be present. The spots are faintly bluish white.

DISTRIBUTION. *Banks Islands*: Ureparapara, ♂ 1; Valua, ♂ 1, ♀ 1; Vanua Valava, ♂ 4, ♀ 2; Mota, ♂ 1; Merelava, ♂ 1; Gaua, ♂ 10, ♀ 1. "*New Hebrides*", ♂ 6, ♀ 1; Espiritu Santo, ♂ type +30, ♀ 15; Malo, ♂ 4; Aore, ♂ 1, ♀ 1; Aoba, ♂ 10; Pentecost, ♂ 8; Malekula, ♂ 19, ♀ 5; Epi, ♂ 18, ♀ 5; Tongoa, ♂ 1; Efate, ♂ 2, ♀ 1. Total ♂ 118, ♀ 32.

No. 69, *rileyi*.

This well-spotted and elegant subspecies is the last of the series of small forms of *boisduvalii*. It differs from all others by the invariable presence of F.W. D.10 below, and very often above as well; D.11 is frequent and even D.12 occurs. Quite exceptionally there are no spots at all above. On H.W. underside D.3-4 and the cell-spot may be slightly blued, as in the holotype.

DISTRIBUTION. "*New Caledonia*", ♀ 1; Noumea, ♂ 2, ♀ 1; "*Loyalty Isles*", ♂ 4; Lifu, ♂ type × 29, ♀ type +8; Uvea, ♂ 1. Total ♂ 37, ♀ 11.

No. 70, *herrichii*.

With this Fijian subspecies the size returns to that of *fraudulenta*. It is boldly white-marked but the number and size of the spots is extremely variable, and

the minimal specimens are transitional to *mangoensis* (*vide infra*). A feature upon which Poulton laid much stress in 1924 is the extension of S.3 on F.W. above to meet D.3 broadly so as to make a conspicuously large white mark: in minimal specimens S.3 is narrowed internally and may not even reach D.3. On the F.W. D.10 is by no means always present above but is only exceptionally absent below: D. 11 is similar. In the maximal male, on F.W. underside, the end of the brand is marked by white, making a spot in 1b. Submarginal 4 on F.W. drops out in minimal specimens. In a maximal female, on the underside of both wings, the cell-spot and all the discals are bluish white.

DISTRIBUTION. The ♀ type was from "Fiji". *Western Fiji*: Yasawa group, ♂ 2, ♀ 1; Viti Levu, ♂ 80, ♀ 42; Moturiki, ♀ 1; Ovalau, ♂ 26, ♀ 13; Makongai, ♂ 1; Vanua Levu, ♂ 8, ♀ 7; Taveuni, ♂ 10, ♀ 3; Koro, ♂ 5; Ngau, ♂ 1; Kandavu, ♂ 1. *Lau Group*: Lakemba, ♂ 1; Thithia, ♂ 1. *Ellice Group*, ♀ 1. Total ♂ 136, ♀ 69. The occasional occurrence of *herrichii* in Fiji Lau (Thithia and Lakemba) does not mask the fact that this is the western race. The single record from the Ellice group is not impossible. In addition, forms transitional to *mangoensis* by reduction of the white spots come from the more eastern isles: Koro, ♂ 16; Ono, ♂ 4; Kandavu, ♂ 4; Thithia, ♂ 1. Total ♂ 25.

No. 71, *boisduvalii*.

This nomino-typical form was found by Talbot (1921) to be merely an intermediate between *herrichii* and *mangoensis*. The type is not available but two males at Oxford seem to conform to the description. On F.W. the spots are small and dyslegnic, suffused with black; on H.W. they are clearer. The large submarginal in F.W. 3 is inwardly pointed and forms a small arrowhead. On the underside the spots are less dyslegnic, but are small.

DISTRIBUTION. *Fiji*: Koro, ♂ 2.

No. 72, *mangoensis*.

Reduction of the white spots of *herrichii* has gone further than in *boisduvalii* so that in the minimal male there are no spots on the upper side and the form has a resemblance to *fraudulenta* from which it can be distinguished by F.W. D.2 below not being elongated into a bar.

Poorly marked specimens from Wallis Island resemble *torvina* from Tanna. The series from Wallis Island have F.W. D.10 on the underside much more often shown than in other examples of *mangoensis*; only one, a female, altogether lacks it. As in *boisduvalii* the spots are better defined on the underside.

DISTRIBUTION. *Western Fiji*: Koro, ♂ 4, ♀ 1. *Lau Group*: Moala, ♂ 4, ♀ 1; Thithia, ♂ 4, ♀ 3; Mango, ♂ 3, ♀ type; Munia, ♂ 3; Vanua Mbalavu, ♂ 17, ♀ 3. Also ♂ 1 from "Kanaua" which I cannot place. *Wallis Island*, ♂ 3, ♀ 5. Total ♂ 39, ♀ 14.

No. 73, *eurianassa*.

This well defined species has been split by Fruhstorfer (1910) into three forms which are not here separated. The difference lies in the width of the white band and the clouding over with the brown colour, but the forms so easily grade one into another that it may be impossible to decide to which form any particular specimen should be assigned. Examples of all the forms occur together on Fergusson Island.

It is exceptional for any separate spots to occur on the upper surface, but in maximal specimens of both sexes there are traces of F.W. discals 2, 3, 4. On the underside there is, exceptionally, a trace of F.W. D.10 in both sexes; on H.W. D.7 only occurs in the maximal specimens and D.1c is only seen in the maximal female. The cell-spot is always present on H.W. beneath. The yellowish tint ascribed to "*cumaxa*" is dubious; I noted in the type specimen that the white band is clouded with brown, especially on F.W. in areas 7-9, and narrowed: but it did not seem to me to be yellowish.

DISTRIBUTION. *New Guinea*, ♂ type + 45, ♀ 25. *Louisiade Archipelago*: Samarai, ♂ 1, ♀ 1; Nivani, ♂ 5; Sudest, ♂ 23, ♀ 2; Rossell, ♂ 28, ♀ 2; St. Aignan, ♂ 4, ♀ 2. "*D'Entrecasteaux Archipelago*", ♂ 3; Goodenough, ♂ 16, ♀ 13; Fergusson, ♂ 10, ♀ 9; Normanby, ♂ 1. Total ♂ 137, ♀ 54.

No. 74, *inconspicua*.

This is the first of the *doleschalii* section of the *sylvester* complex. True *doleschalii* has, in the male, the submarginals of the F.W. not dark blue but purplish white or even white; this form is not found on the islands here considered, although abundant in New Guinea.

Butler's *inconspicua* (which I consider includes *immaculata* Butler, 1878, *suada* and *crithon* Miskin, 1890, *limbata* and *tarnis* of Fruhstorfer, 1910) occurs with *doleschalii*. The spots are usually absent from the upper side but maximal males and females have traces of blue submarginals on F.W. 6-7 in the male and 2-9 in the female. Fruhstorfer's *limbata* tends to have paler margins on the upper side, especially on H.W., which, when more accentuated produces his form *agema*. The forms *limbata* and *tarnis* are from Waigeu and Jobi; *inconspicua* and *immaculata* are widely spread through New Guinea and some of the islands to the west of New Guinea.

Mention is made of this assemblage because there is in the national collection a male labelled "Torres Straits". A total of ♂ 50, ♀ 11 has been examined, but for the purposes of this paper *limbata*, *tarnis* and *suada* are not included.

The form *crithon* from Cape York was described by Miskin (1890) as velvety black without spots above, and having on the underside two discals on F.W. and five on H.W.; cell-spots were not mentioned. Waterhouse & Lyell (1914) "consider it probable that *crithon* is identical with *Stictoploea immaculata* from New Guinea", and say that in the far north of Australia it intergrades with typical *sylvester*; four males and two females are recorded from Cape York and Darnley Island. Their figures show *crithon* spotless above: the male has on the underside small F.W. D.2-3 and cell-spot; on H.W. small D.2-6 and cell-spot. The female has slightly larger F.W. D.2-3, very small 4, no cell-spot; on H.W. small D.2-6 and minute cell-spot. Waterhouse (1932) figures a male *crithon* with even fewer spots beneath than the minimal number given in the table: on F.W. only D.2-3, and no spots on H.W. It is significant that in *inconspicua*, as in *corinna*, there is reported to be greater variability in the extreme north; this seems to imply constant introduction of new strains from across the sea to the north.

DISTRIBUTION. *Dutch New Guinea*, ♂ 26, ♀ 3 + 2 trans. to *agema*. ex *German New Guinea*, ♂ 14, ♀ 2. *British New Guinea*, ♂ type *immaculata* + 7, ♀ types of *immaculata* and *inconspicua* + 2. *Torres Straits*, ♂ 1. Total ♂ 49, ♀ 11 + 2 trans. to *agema*.

No. 75, *moesta*.

Under this name are included the poorly spotted forms with small, dark blue, submarginals without white suffusion on upper side of F.W. in areas 6-7 at least; H.W. without spots. The presence of F.W. D.10 below is exceptional.

DISTRIBUTION. *Dutch, British and ex-German New Guinea*, ♂ 21. The ♂ type is from Dorey. *Santa Cruz Islands*: Matema, ♂ 2. Total ♂ 23.

No. 76, *melander*.

Smaller than *moesta*, dusky, poorly spotted, *melander* can be separated by its distribution. The female may have discals on F.W. upper surface; the F.W. submarginals in the male are blue, in the female tinged with white. The discals and cell-spot on H.W. underside may be blue.

No specimens corresponding to the types have been seen from New Guinea, and the islands of the Santa Cruz group on which *melander* occurs do not include Matema, where *moesta* is found.

DISTRIBUTION. *Santa Cruz Isles*: Santa Cruz, ♂ type +3, ♀ type +1; Utupua, ♂ 1, ♀ 1; Vanikoro, ♂ 1, ♀ 1. *Banks Isles*: Reef Island, ♂ 2. Total, ♂ 8, ♀ 4.

No. 77, *magnipunctata*.

The name *magnipunctata* was given to this as a form of *tristis* with larger spots; now that *tristis* itself is classed as a form of *sylvester* (*sens. lat.*) the name has lost its significance. The elongation of the H.W. submarginal paired-spots is very noticeable, and, in the female especially, the larger size of F.W. submarginals and discals.

DISTRIBUTION. *Banks Islands*: Ureparapara, ♂ type +2; Pakea, ♂ 2, ♀ type +3. Total ♂ 5, ♀ 4.

From the D'Entrecasteaux Archipelago, Fergusson Island, there is in the Oxford Museum a male which is transitional in that it has large anterior submarginals in F.W. 6-7 but only minute spots in 2-3. The paired submarginals of H.W. however, in 1c-3 are larger than in most specimens of *tristis*. More material from Fergusson would be valuable, as the *tristis* forms of *sylvester* are not otherwise known from the D'Entrecasteaux group.

No. 78, *tristis*.

It might seem legitimate to claim that as *tristis*, *inconspicua*, *moesta*, *melander* and *magnipunctata* seem closely connected by intermediates it would be justifiable to treat all as synonyms of *tristis*. Yet the geographical distribution supports the continuance of these names.

Tristis is the form most commonly seen in collections. The following spots have been noted as exceptional: ♂ F.W. below, S.8; ♀ F.W. above, S.4 and D.7; below, S.8 and D.8. The paired H.W. submarginals are not rounded but slightly prolonged towards the base; as they become longer they lead to *magnipunctata*.

DISTRIBUTION. *Santa Cruz Isles*: Matema, ♂ 1. *Torres Isles*: Hiw, ♂ 10, ♀ 2 (for an abnormal ♀ *vide infra*); Tegua, ♂ 13, ♀ 5. *Banks Isles*: Reef Island, ♂ 2 (poorly spotted, trans. to *melander*). "New Hebrides", ♂ 8, ♀ 5; Malo, ♂ 1, ♀ 1; Aoba, ♂ 2, ♀ 3 (+ trans. to *magnipunctata* ♂ 1, ♀ 1); Malekula, ♂ 8, ♀ 3; Epi, ♂ 4; Efate, ♂ 1; Aneityum, ♂ type. *New Caledonia*, ♂ 2, ♀ 1. Total ♂ 54, ♀ 22. An unusual locality is Matema: Reef Island is interesting as the usual form in the Banks Group is *magnipunctata*. The abnormal female was captured by J. J. Walker on Hiw. The F.W. above has faint traces of blue S.2-3, bluish white 6-7 and white D.4-6, 9-10. The H.W. has no spots. Beneath, F.W. has very small S.6-7, white D.2-6, 9-10 and a large white

cell-spot. H.W. has no A. or S. but large white discals, a long streak in 1b, a pair of streaks in 1c, large 2-7 and cell-spot. The poorly-spotted upper surface with anterior discals alone developed on F.W. is not matched in any other specimen.

No. 79, *pelor*.

A form of *sylvester* with reduced spotting, especially admarginals. Variable, like others in North Australia.

DISTRIBUTION. Musgrave (1948) gives "in the Northern Territory at Darwin, Daly and Roper Rivers". I have examined specimens as follows:—"New Holland", ♂ 1, ♀ 1; Cape York, ♀ 1; Adelaide River, ♂ 1; Port Darwin, ♂ 15, ♀ 7. Total ♂ 17, ♀ 9.

No. 80, *sylvester*.

The following markings are exceptional. F.W. D.12 on male below, on female above and below. H.W. below S.7 in both sexes. The maximal male and most females have H.W. S.1b-6 fused into large patches; in the maximal female H.W. areas 1a-1b are filled with white.

DISTRIBUTION. Musgrave (1948) gives "Prince of Wales, Banks, and Darnley Isles in Torres Straits to Mackay in Queensland".

There are in the national collection two males and one female from "Port McQuarie" but this is considered to be open to doubt. I have examined the following specimens:—"New Holland", ♀ 2. "North Australia", ♂ 6, ♀ 3; Thursday Island, ♀ 1; Port Albany, ♂ 1. "Queensland", ♂ 3, ♀ 2. North Queensland: ♂ 6, ♀ 3; Cape York, ♂ 5, ♀ 2; Cedar Bay, ♂ 2; Horn Island ♀ 1; Cooktown, ♂ 3; Cairns, ♂ 12, ♀ 11; Kuranda, ♂ 9, ♀ 4; Little Mulgrave River, ♂ 2; Mackay, ♂ 2. Total ♂ 51, ♀ 29.

No. 81, *dardanoides*.

A variation with spots reduced by dusky suffusion, especially on H.W. The F.W. has the shape of that of *pelor* rather than of *sylvester*.

DISTRIBUTION. "North Australia", ♂ 1; Port Darwin, ♀ 3. "Queensland", ♂ 1, ♀ 1. Total ♂ 2, ♀ 4.

No. 82, *treitschkei*.

The variable forms grouped under the specific name of *treitschkei* have proved to be extremely troublesome to sort out, more especially as some "species" have been described from males, others from females and the proper assignment of sexes to each other is very difficult. I have found it impracticable to treat the forms as usual in the tables; very few specimens are exactly like another and not much reliance can be placed upon spot development. A good deal depends upon the general coloration, but in the females the shades of green are confusing and the blue in the males varies much. I have, when only one sex has been described, selected a ne-allotype. The nomino-typical form was described from a male from New Ireland; it is dull purple-black without bronzy reflection above, and blue-black below. The upper side may be spotless, and the spots are never greatly developed. It grades into *caerulescens* and *ursula*. The female is of a rather brassy, hard green with faint blue reflection when viewed obliquely: it is difficult to distinguish it from others which are classed as *caerulescens*. The ne-allotype (in the National Collection) has a slight suffusion with paler scales on F.W. at the end of the cell and in the bases of 3-6, and around the end of the

double spot in 1b. Under-surface of both wings a blacker green, without bronze or blue reflection.

DISTRIBUTION. *Bismarck Archipelago*: Duke of York Island, ♂ 4, ♀ 2; New Ireland, ♂ type + 7, ♀ ne-allotype + 8; Queen Charlotte Island, ♂ 9, + 4; Feni, ♂ 8, ♀ 10. Total ♂ 29, ♀ 25.

No. 83, *eugenia*.

This form, limited to Vulcan Island off the north coast of ex-German New Guinea, seems definite enough to be treated like other species, and I have given maxima and minima. The type is a female, of yellowish green colour like *gaedei*; F.W. S.5-6 are large and white, a feature also found in *ursula* and occasionally in *gaedei*; on H.W. the paired S.3 is joined apically to D.3, though not on the underside. In the maximal female the F.W. cell-spot is dyslegnic above, and doubled below, and the discals are dyslegnic above. The minimal female specimen, if considered without its locality, might be placed as an example of *aenea* from the Solomons.

DISTRIBUTION. Vulcan or Manam Island, ♂ 5, ♀ 7.

No. 84, *dampierensis*.

Rothschild in 1915 described as "*intermedia*" four males and two females "exactly intermediate between *olivacea* [= *gaedei*] and *eugenia*". The name *intermedia* must sink, as pre-occupied by Moore, and I now apply the name *dampierensis*. The male type, but not others, has F.W. apical submarginals large, eulegmic, and white; the underside shows H.W. discals well marked and rather larger than in *gaedei*; small S.4-6 may show on H.W. upper side, pure white and conspicuous. The general coloration above is deep blue-black. One of the females is much like *gaedei*, the other a darker green more like that of *aebutia* Fruhstorfer, 1910; the former has no F.W. S.5-6 on upper side but these are present in the other.

DISTRIBUTION. Dampier or Karkar Island, ♂ 4, ♀ 2.

No. 85, *ursula*.

The male is much like that of *t. treitschkei*, dull purple-black without any blue gloss above, and blue-black below. The female is dull bronzy green, darker than *gaedei* and nearer to *viridis*. Submarginals 5-6 on F.W. seemed to be a characteristic, but they do occur on other forms and when they are very small there is little to distinguish *ursula* from *t. treitschkei*, and they occur together. I include *biformis* Butler, 1882, in *ursula*; Butler wrote that it was doubtless a geographical representative of *treitschkei*; the type came from Duke of York Island.

DISTRIBUTION. "*Admiralty Isles*", ♀ 3; D'Entrecasteaux Reef, ♂ type + 5, ♀ type + 2; Manus, ♂ 4, ♀ 4; Los Negros, ♂ 5, ♀ 5. *Bismarck Archipelago*: New Ireland, ♂ 3; Duke of York Island (as *biformis*), ♂ 1, ♀ 2; St. Mathias Island, ♂ 4, ♀ 4; Squally Island, ♂ 2, ♀ 2. *New Guinea*: Finschhafen, ♀ 1. *Louisiade Archipelago*: Rossell Island, ♂ 2, ♀ 1; St. Aignan, ♂ 1, ♀ 1. *D'Entrecasteaux Archipelago*: Fergusson, ♀ 1. Total ♂ 28, ♀ 27.

No. 86, *gaedei*.

Described from Humboldt Bay by Grose Smith (1894) as *olivacea*. Bryk (1937) substituted *gaedei* since *olivacea* was pre-occupied. The male is dark greenish

black above with a slightly bluish tint on the H.W., by which it differs from *aebutia* Fruhstorfer, 1910, in which the F.W. has the same colour as the H.W. Beneath it is not such a blackish blue as *t. treitschkei*. The female is uniform olive green without blue reflection, the spots dull white. The presence of F.W. S.5-6 was discussed under *ursula*.

The form "*hageni*" Bryk, 1937, is a male without spots above. Fruhstorfer's "*pulverulenta*" is merely a female with spots on upper side large and dyslegnic.

The form *gaedei* abounds in New Guinea; I have seen specimens from Arfak and Dorey to Port Moresby.

DISTRIBUTION. *New Guinea*, ♂ type + 60, ♀ type + 50. *Bismarck Archipelago*: New Britain, ♀ 1; New Ireland, ♀ 1. Total ♂ 61, ♀ 53.

No. 87, *caerulescens*.

In the absence of type specimens the description given by Pagenstecher (usually considered the author) does not convey much. The only salient point is the intense blue colour which is also shown by the triad included under the name *jessica* (No. 90). It seems that the authorship of the name should be ascribed to Ribbe and not to Pagenstecher, who merely wrote in 1894 (*Jahrb. Nassau. Ver. Nat.* 47, 73) that Ribbe had sent him a series of this amazingly varying species which he calls *caerulescens* from Mioko. No specimen is like the other, they differ in the number of spots. This hardly seems to serve as a description.

Ribbe in 1898 (*Soc. Ent. Zurich XII*, Jahrgang No. 23, p. 177) describes "local forms" of *treitschkei* from Neu Pommern and Neu Lauenberg as differing greatly by a striking blue iridescence in both sexes; the white spots more abundant than in *treitschkei* on under- as well as on upper-side. The females have a whitish tint on the F.W. *Caerulescens* is larger than *treitschkei*. Amongst specimens from Neu Lauenberg are some differing strikingly in markings. The males have well-marked elongated spots on F.W., and H.W. has a row parallel with the outer margin. The females have white spots on F.W. which, toward the margin and base, merge into the blue ground-colour. On H.W. the white row of spots is much more developed than in *caerulescens*, and this form is called *var: albopunctata*. It seems highly probable that these last mentioned specimens at any rate come under *jessica*.

Using *caerulescens* for forms merely characterized by the intense blue I record the following specimens examined.

DISTRIBUTION. *Bismarck Archipelago*: New Britain, ♂ 28, ♀ 23; Duke of York Island, ♂ 3, ♀ 5; Queen Charlotte Island, ♂ 9, ♀ 4. Total ♂ 40, ♀ 32.

No. 88, *eulegnica*.

The sharply marked spots suggested the name for this new geographical race. Male type: smaller than the average size of *treitschkei* forms, and with shorter F.W. Intense blue-black above, but not so bright as in *caerulescens*: cell-spot pure white. Brand very small, bluish-white. On underside the spots very sharply defined and mostly bluish white; ground-colour deep blue-black. The female allotype has a short F.W. like the male; it is bluer than other females of the *treitschkei* complex, but with more steely-green reflection than in the male. The

H.W. spots above are white and eulegmic, especially on the underside where they are larger. The spots on the F.W. which tend towards bluish-white above are pure white below. Among the females from Nissan Island one is much less blue and comes near to a female *gaedei*. Both types collected by A. F. Eichhorn, Aug. 1924, are in the Rothschild collection of the British Museum (Nat. Hist.).

DISTRIBUTION. *Bismarck Archipelago*: St. Mathias Island, ♂ 7, ♀ 7; Squally Island, ♂ 2, ♀ 2; Nissan Island, ♂ type +8, ♀ type +8. Total ♂ 18, ♀ 18.

No. 89, *viridis*.

Butler's type is supposed to have come from Thursday Island but, as Waterhouse & Lyell (1914) say "no other example has been taken within Australian limits . . . we therefore consider it almost certain that this Island was the place of export but not the place of capture".

Fruhstorfer (1910) described *decia* from a male from Milne Bay, and females associated in his collection with his type agree with Butler's *viridis*. The name *decia* is sunk, and Fruhstorfer's male type (in British Museum (Nat. Hist.)) is taken as the male ne-allotype of *viridis*.

Butler's female type is very strongly dark bronzy green; the male "*decia*" is dull blue-black with faint blue gloss, and on the underside blackish bronze-green. On underside of H.W. the spot in 2 is horse-shoe shaped, indicating union of a discal with paired submarginal.

DISTRIBUTION. Widely distributed in British New Guinea. (I have seen two from ex-German New Guinea but none from Dutch territory. From Biak three specimens have been seen.) *British New Guinea*, ♂ ne-allotype +22, ♀ 26. *Bismarck Archipelago* (Fruhstorfer collection): New Ireland, ♀ 2. *Louisiade Archipelago*: Samarai, ♂ 3, ♀ 4; Doimi Islet, ♂ 1; Gesila Islet, ♀ 3; Kwato Islet, ♀ 1; St. Aignan, ♀ 2; Nivani, ♀ 2. *D'Entrecasteaux Archipelago*: Fergusson, ♂ 2 (trans. to *ursula*, ♀ 1); Goodenough, ♂ 1, ♀ 6. *Trobriand Archipelago*: Woodlark, ♂ 11, ♀ 9; Egum (Yanarba), ♂ 1, ♀ 5. Total ♂ 42, ♀ 60 +1 transitional. In addition I have seen the following specimens which can only be classed as transitional to *jessica*. *Solomons*: San Cristobal, ♀ 1 (F.W. of form *lorenzo*, H.W. spotless). *Santa Cruz* group: Vanikoro, ♀ 3. Total, ♀ 4.

No. 90, *jessica*.

The male type of Butler's *jessica* (1896) was supposed to have come from "Fiji", which is out of the question. I find it impossible to draw a sharp line between *lorenzo-jessica-erimas*, putting these three forms in order of increasing development of white patches. But it seems desirable to tabulate the type specimen of each form, with selected ne-allotypes. Both *lorenzo* and *erimas* occur in the Bismarck Archipelago; the type of the former came from "South Sea Islands", of the latter from New Ireland.

DISTRIBUTION. *Bismarck Archipelago*: Witu, ♂ 13, ♀ 15; New Britain, ♂ 9, ♀ 1; New Ireland, ♂ 25, ♀ 21; Feni, ♀ 2. *Louisiade Archipelago*: St. Aignan, ♂ 6, ♀ 3; Sudest, ♂ 5, ♀ 8; Rossell, ♂ 9, ♀ 5. *D'Entrecasteaux Archipelago*, ♀ 2; Fergusson, ♀ 1. *Solomons*: San Cristobal, ♂ 3, ♀ 3; Ugi, ♀ 1. *Banks Isles*: Pakea, ♂ 3, ♀ 2. "*New Hebrides*", ♂ 7, ♀ 5; Espiritu Santo, ♂ 2, ♀ 2; Aore, ♂ 2, ♀ 2; Malekula, ♂ 3, ♀ 4; Mai, ♂ 1, ♀ 1; Efate, ♂ 4, ♀ 2. *New Caledonia*, ♂ 1, ♀ 1. Total ♂ 93, ♀ 81.

This is a remarkable distribution. New Guinea is left out: the forms appear in Bismarck Archipelago but after D'Entrecasteaux are not known in any of the Solomon Islands except San Cristobal and Ugi, of which the other fauna is highly peculiar. The greater number of the

Solomon Islands, however, are inhabited by the next form, *aenea*. From the end of the Solomons group *jessica* forms continue, via Banks Isles, into New Hebrides and even New Caledonia.

No. 91, *aenea*.

Described by Butler from both sexes in the Solomons this is the characteristic form of *treitschkei* on these islands. The male, very like *t. treitschkei*, is dull bronzy blue, not so bright as in *jessica*; the female is rather like *gaedei*.

DISTRIBUTION. "*Louisiades*", ♂ 1; Nivani, ♂ 1. *D'Entrecasteaux Archipelago*: Fergusson, ♂ 1. *Trobiand Archipelago*: Woodlark, ♂ 3, ♀ 3, plus ♂ 3 trans. to *suffusca*. "*Solomons*", ♂ type ♀ type; Bougainville, ♂ 12, ♀ 10; Fauro, ♂ 5, ♀ 3; Shortlands (with Alu), ♂ 5, ♀ 8; Kundi-kaboko, ♀ 1; Choiseul, ♂ 1; Vella Lavella, ♀ 5; Ganongga, ♂ 1, ♀ 2; Kolombangara, ♂ 1, ♀ 1; Rubiana, ♂ 1; Rendova, ♂ 3, ♀ 3; Ysabel, ♂ 5, ♀ 8; Russell Isles, ♂ 20, ♀ 32; Savo, ♂ 1; Undeka, ♂ 1; Florida (with Tulagi), ♂ 36, ♀ 13; Guadalcanal (with Aola), ♂ 23, ♀ 31; Malaita, ♂ 11, ♀ 10; Maramasike, ♂ 5; Ulawa, ♂ 3, ♀ 2. *Santa Cruz Isles*: Utupua, ♂ 1. Total ♂ 142 + 3 transitional, ♀ 133. It will be noted that none has been seen from New Georgia itself, though Rendova provided one specimen. The point of great interest is that *aenea* is lacking from San Cristobal and Ugi, the only islands in the Solomons from which *jessica* has been recorded. The single male from the Santa Cruz group represents the furthest extension of this common form.

No. 92, *suffusca*.

This name has been devised for some peculiarly dull brownish specimens from Kiriwina. The male is brownish black without any blue or green reflection on the upper side; below there is a slight bronze sheen. The sex stripe on the male is short, and white like the spots.

DISTRIBUTION. *Trobiand Archipelago*: Kiriwina, ♂ type + 2, ♀ type. Total ♂ 3, ♀ 1. The type, ex Fruhstorfer, is in the British Museum (Nat. Hist.): paratypes and allotype in the University Museum, Oxford. Three males from Woodlark were noted, under *aenea*, as transitional to *suffusca*. The table (p. 110) gives the distribution of each of the forms of *treitschkei*.

No. 93, *asyllus*.

Under this name *laurentia* Fruhstorfer, 1910, is sunk; it is merely a poorly spotted specimen. In the list of localities for *asyllus* (1) indicates that "*laurentia*" occurs there. This species is very easy to identify; it is remarkable for never having a cell-spot although all the three series of spots are very well developed. The upper side of F.W. almost invariably shows D.10, and this is the only spot on the upper side of "*laurentia*"; it is absent from the minimal male. D.11 appears as an exception on the underside of the female allotype.

DISTRIBUTION. Entirely confined to the Solomons, from Bougainville to Guadalcanal, but absent from certain important islands. A male from the Oberthür collection has data "New Guinea, Dorey Bay" which is highly improbable.

"*Solomons*", ♂ 2, ♀ 8; Bougainville, (1) ♂ 27, ♀ 12; Shortlands, ♂ 1, ♀ 1 + (1) type; Alu, ♂ type + 10, ♀ type + 1; Choiseul, (1) ♂ 5, ♀ 3; Vella Lavella, (1) ♂ 11, ♀ 10; Ganongga, (1) ♂ 1, ♀ 1; Gizo, (1) ♂ 3, ♀ 1; Kolombangara, (1), ♀ 1; Arundel, (1), ♂ 1; New Georgia, (1), ♂ 4, ♀ 1; Narovo, (1), ♀ 1; Rendova, ♂ 2, ♀ 2 (all (1)); Rubiana (1), ♂ 1, ♀ 2; Ysabel, (1), ♂ 6, ♀ 5; Islet near Ysabel, (1) ♀ 1; Russell Isles, ♂ 1; Florida (with Tulagi), ♂ 9, ♀ 9; Guadalcanal (with Aola), ♂ 5, ♀ 28. Total ♂ 90, ♀ 89.

Note that the islands lacking *asyllus* are Malaita, Ulawa and those at the eastern end of the group.

Forms of <i>Euploea treitschkei</i>													
<i>suffusa</i>	<i>aenea</i>	<i>jessica</i>	<i>viridis</i>	<i>eulegnica</i>	<i>caerulescens</i>	<i>gaedei</i>	<i>ursula</i>	<i>dampierensis</i>	<i>eugenia</i>	<i>treitschkei</i>			
+									+		Vulcan I.	}	Papua Adm.
											Dampier I.		
											Admiralties		
			+					+			Witu		
			+			+	+				New Britain	}	Bismarck Archipelago
						+		+		+	Duke of York		
			+	+		+	+	+		+	New Ireland		
						+				+	Queen Charlotte I.		
					+			+			St. Mathias	}	Bismarck Archipelago
					+			+			Squally I.		
			+							+	Feni		
					+						Nissan		
		+		+							Samarai	}	Louisiades
			+	+				+			Nivani		
			+	+							St. Aignan		
			+					+			Sudest		
		+	+	+							Rossell	}	D'Entrecasteaux
				+				+			Goodenough		
		+	+	+							Fergusson		
		+		+							Kiriwina		
				+							Woodlark	}	Trobriand
				+							Egum		
		+	+	+	(trans.)						Solomons (see table p. 134)		
		+		+	(trans.)						Utupua		
			+								Vanikoro		New Caledonia
			+								Pakea		
			+								Espiritu Santo		
			+								Aore		
			+								Malekula		
			+								Mai		
			+								Efate		
			+								New Caledonia		

No. 94, *gerion*.

This extremely rare subspecies has previously been known only by the type, a female. The collection which Dr. Ross of the California Academy of Sciences so kindly lent me contains the male ne-allotype. This has a certain resemblance to *pronax* in the shape of the wings, especially the straighter edge to the H.W. But the much smaller, bluish, brand, measuring only $1\frac{1}{2} \times \frac{1}{2}$ mm., and the whitish speculum, covering almost the whole cell on H.W., distinguish *gerion* from *pronax*.

On H.W. upper side white suffusion masks the submarginals, except for the pair in 3 and the single 4. The white makes an ill-defined band through areas 2-1c-1b to the anal angle. Below, the F.W. has 1a white. On H.W. a broad white border runs from S.5 back to the anal margin, where it widens. F.W. discals 5-6 and 10 are bluish, the others white; all spots on H.W. are blue. The female type shows S.4-8 on underside F.W.; on H.W. the only visible spots are S.6-7.

DISTRIBUTION. *Solomons*: Malaita, ♂ ne-allotype, ♀ type.

No. 95, *dudgeonis*.

Described from Humboldt Bay in 1894 by Grose Smith. Rothschild (1915) described as *vulcanica* specimens which do not materially differ from *dudgeonis*, and the name is sunk. These specimens have the F.W. submarginals smaller and a little more obscured than most examples of *dudgeonis*, but both have the same uniform light brown under-surface with spots reduced to the minimum. It is possible that *doryca* Butler, 1878, should be the name for all these three.

Grose Smith, as he himself remarked, described rather an abnormal specimen for his female allotype; the F.W. submarginals are pale and diffuse so as to make a pale violet band; such abnormality is seen in other forms of *tulliolus*. Most of the females, as in Rothschild's "*vulcanica*" have the spots like those of the male. There is a strong purple gloss on the rather dark F.W. and posterior half of H.W.

DISTRIBUTION. "*New Guinea*", ♂ 1. *Dutch New Guinea*, ♂ 2; "*Hollandia*", ♂ 1; Humboldt Bay, ♂ type +4, ♀ type +4; Cyclops Mountains, ♂ 1. "*Northern New Guinea*", ♂ 2; Madang, ♂ 1, ♀ 1; Vulcan Island, ♂ type, ♀ type "*vulcanica*". Total ♂ 14, ♀ 7.

No. 96, *tulliolus*.

The ♂ type is the beautiful figure in Jones "Icones" in the Oxford University Museum (Hope Dept.), vol. 3, pl. 67 (misquoted as 69 by Fabricius, 1793, *Ent. Syst.* 3 (i) 41.). Butler's ♀ type of "*turneri*" (1878), which is a synonym, is taken as ne-allotype. This, the nominotypical race, is on the whole stable, and well defined from other races in our area by the F.W. large submarginals, general absence of submarginals on H.W., and the circular shape of F.W. D.2 below, which often tends to be oval in other races. F.W. D.10 is always present above, and often conspicuous. D.12 is seen in maximal ♂ and ♀, but curiously enough D.11 is absent, even on the underside. This race grades into *darchia* (No. 100).

DISTRIBUTION. Musgrave (1948) gives "from Darnley to Mackay". Waterhouse & Lyell (1914) say it is a great rarity in the Brisbane district. A specimen in the Rothschild collection from "New South Wales" needs confirmation. The *tulliolus* complex has an enormous distribution in Malaysia, Aru, and the Pacific, and on the continent extends into China. It reaches northwards

to the Riu-Kiu Islands, and in the south Pacific reaches North Caledonia and the Loyalties but does not leave the continental shelf. It is *unknown in the Solomons*, a remarkable fact. The Melanesian and Australian forms are generally paler on the underside than Malaysian forms which tend towards reddish brown and have F.W. D.2 larger and transversely elongated. The specimens I have examined come from the following localities.

"Australia", ♂ 1, ♀ 1; North Australia, ♀ 2; Queensland, ♂ 52, ♀ 10; North Queensland, ♂ 2; Thursday Island, ♂ 5, ♀ 14; Darnley Island, ♀ 1; Port Stephen, ♀ 1; Frankland Island, ♂ 2; Cairns, ♂ 1; Moreton Bay, ♂ 1; Rockingham Bay, ♂ 1; Magnetic Island, ♂ 1; Rockhampton ♂ 1, ♀ 2; Port Denison, ♂ 1; Ross Island, ♂ 1, ♀ 1; Brisbane, ♂ 1, ♀ 2; Toowoomba, ♂ 1. In addition, there is an interesting series from Tana in *New Hebrides* (see Poulton, 1927): ♂ 8 collected by P. A. Buxton in 1925 and ♂ 2, ♀ 1 by W. Armstrong in 1926, in all ♂ 10, ♀ 1. Some specimens have F.W. submarginals 5-6 even larger than in Australian specimens: D.10 always present above although only a trace is seen in one male: on the underside it is always present and usually well developed to a degree which contrasts with the specimens of *forsteri* from the same locality. But F.W. D.2 on the underside is not as constant as in Australian specimens: it is absent in six and quite small in the other four, and very small in the single females. By comparison, only in one of six Australian specimens is it lacking. The association of these slightly abnormal *tulliolus* with a series of normal *forsteri* on Tana suggests that a wanderer from Australia has bred with *forsteri*.

Another interesting, and somewhat similar situation, has been brought to light by a collection made at La Foa in *New Caledonia* by Professor Charles L. Remington of Yale who kindly sent them to me. There are six males and eight females. One male and one female are *tulliolus* forms, though not quite typical, suggesting admixture with *adyte* stock. Five males and five females, one male being *in copula* with a female very like itself, are *forsteri* in various degrees of reduction of the F.W. spots; two other females are very near to *adyte* in the brownish coloration, absence of the submarginals from F.W.2 and 3 on upper side, and also of D.10, and on the underside absence of D.2 and D.10. Further, the following specimens are of interest; they may be accidental introductions, or mistaken records:—*Fiji*: Suva, ♀ 1; Vanua Levu, ♀ 1. *Loyalty Isles*: Maré, ♂ 1. An abnormal specimen, brownish like other specimens from the Loyalties but with large F.W. submarginals and D.10 and the under-surface as in *tulliolus*: possibly a hybrid.

Including the above slightly atypical specimens the total seen is ♂ 83, ♀ 36.

No. 97, *goodenoughi*.

Only the type ♀ is known. F.W. submarginals large and white; D.10 absent. Faintly indicated submarginals on H.W. suggest the band in *darchia* (No. 100). On the F.W. underside area 1a is dull brownish white, in 1b-2 there are faintly purplish white patches. Discal 3 is present, flattened antero-posteriorly; this spot is not known in other members of the *tulliolus* complex.

DISTRIBUTION. ♀ type from D'Entrecasteaux Archipelago, Goodenough Island. In British Museum (Nat. Hist.), Rothschild collection.

No. 98, *forsteri*.

The forms now to be discussed, with the F.W. submarginals less developed than in *tulliolus*, and D.10 only shown in maximal specimens, have been rather difficult to classify under their proper names.

Poulton (1924, pp. 598-600) distinguished between the better spotted and the less well spotted forms, describing an extreme example of the latter as "*proto-forsteri*". His type corresponds so closely with Herrich-Schäfer's description (1869) of "*incompta*" that if it is desirable to consider poorly spotted specimens as a form separate from *forsteri* they should bear the name *incompta*. The maximal

female of *forsteri* is very near to *tulliolus*, having F.W. S.5-8 large and contiguous, but D.10 is less developed. On the other hand there is every grade from *forsteri* to *incompta*, and the placing of a specimen is often a matter of personal predilection. No type specimen of *incompta* was available. The description alludes to trifling differences in shape from "*seriata*". At the base of vein R.8 on F.W. there is a patch of blue scales, otherwise there are no spots on F.W., which shows dark violet gloss in certain lights. No mention is made of spots on the underside except three white dots at the root of the H.W. (Such spots are common to most *Euploea*.) Herrich-Schäfer precedes this description with notes on "*seriata*" which he compares with *pollita* and *ledereri* (both of which have well developed F.W. submarginals), being apparently unfamiliar with *tulliolus*. It must be said that in "*seriata*" the spots are not appreciably larger anteriorly, and in 1b the spot is double. (This is much more obvious in "*seriata*" than in *tulliolus*.) A difficulty is again introduced by Herrich-Schäfer's locality for his type, "Vanua Valava"—a difficulty discussed by myself in 1942 (p. 137). The conclusion then reached, that Vanua Mbalavu in Fiji Lau was meant, is rendered more likely by the form under discussion, well known from that island, and the *only* form of the *tulliolus* complex recorded from there. It is not known from Vanua Lava in the Banks Islands which *might* be supposed to be the island indicated by Herrich-Schäfer.

DISTRIBUTION. The presence of the form *incompta* is indicated by (i) after the number of specimens in any locality.

Fiji: *Yasawa Group*: Yasawa, ♂ 1; Waisala, ♂ 1, ♀ 1; Naviti, ♀ 2; Viti Levu, ♂ 31, ♀ 13; Suva or Levuka, ♂ 2, ♀ 2 + (i) ♀ 1; Moturiki, ♀ 1; Ovalau, ♂ 6, ♀ 2 + (i) ♂ 1; Vanua Levu, ♂ 18, ♀ 6 + (i) ♂ 4, ♀ 1; Taveuni, ♂ 3, ♀ 2 + (i) ♂ 1; Koro, (i) ♂ 3; Kandavu, ♀ 2 + (i) ♂ 1; Matuku, (i) ♂ 1; Totoya, ♀ 1 + (i) ♂ 1; Moala, ♂ 4, ♀ 1 + (i) ♂ 3; Lakemba, ♂ 13, ♀ 2 + (i) ♂ 1; Nairai (Naiau), (i) ♂ 1; Thithia, (i) ♂ 7, ♀ 2; Mango, (i) ♂ 8, ♀ 4; Munia (i), ♂ 10, ♀ 1; Vanua Mbalavu, (i) ♂ 31, ♀ 4; Naitamba, (i) ♂ 1. Reference has been made to *tulliolus* on Tana: associated with them is typical *forsteri*, captured at the same time by P. A. Buxton, 1925, ♂ 4, ♀ 1 and W. Armstrong, 1926, ♀ 2. The F.W. submarginals, variable in size, are all smaller and darker than in *tulliolus*: the amount of purple shown is very variable but may be almost nothing in both sexes. Neither sex has F.W. D.10 above or below, or D.2 below, thus contrasting with *tulliolus*: in *forsteri* from other localities D.10 is weakly developed and often absent, likewise D.2.

The collection from *New Caledonia* received from Prof. Charles L. Remington has been mentioned under *tulliolus* previously. The *forsteri* forms, ♂ 5, ♀ 5, must be added to the figures given above. Total *forsteri* ♂ 88, ♀ 43; "*incompta*" ♂ 74, ♀ 13.

A specimen which must be for the present regarded as doubtful, is a *forsteri* from Hewitson in the national collection, with label "Port Denison". This is on the Queensland coast at about 20°. I have seen a typical *tulliolus* from Port Denison in the Rothschild collection.

No. 99, *adyte*.

This small, brownish, race is very near *incompta*, and the collection made by Professor Charles L. Remington at La Foa, New Caledonia, shows intergrading specimens. Typical *adyte* has almost no purple tint, especially in the female, and the small submarginals, almost equal in size, are only glossed with purple in the anterior areas of the male.

DISTRIBUTION. *New Caledonia*, ♂ type +1, ♀ 3. *Loyalty Isles*: Lifu, ♂ 17, ♀ 11; Uvea, ♂ 1 +1 very near *incompta*, Maré, ♀ 2. Total ♂ 21, ♀ 16.

No. 100, *darchia*.

The specimens I have seen do not show much variability; Waterhouse & Lyell, however (1914, p. 23), say it is a variable species, especially in the H.W. spots. A cell-spot is shown only exceptionally; the paired H.W. submarginals tend to complete fusion. There is little purple gloss in the male and none in the female. Enlargement of the *posterior* F.W. submarginals, with 5-6 smaller, suggests affinity with *pyres* rather than with *tulliolus* forms. On the upper side *darchia* somewhat resembles *arisbe catilina* Fruhstorfer, 1904, of Dammer Island, but in *darchia* F.W. D.2 on the underside is often missing while it is present in *catilina*, and when present in *darchia* is smaller.

DISTRIBUTION. "New Holland", ♂ 1, ♀ 1; Australia, ♂ 2, ♀ type of "*priapus*"; Queensland, ♂ 1; Darwin, ♂ 19, ♀ 10; Port Essington, ♂ type of "*priapus*". Total ♂ 24, ♀ 12.

No. 101, *niveata*.

In this form the H.W. admarginals have fused with the submarginals to make large patches. F.W. D.12 may be present in maximal specimens.

DISTRIBUTION. Waterhouse & Lyell (1914) give "Cape York, Thursday Island, Darnley Island, Cooktown, Cairns, Kuranda, Mackay". The specimens I have seen come from "*Australia*", ♂ 2, ♀ 1; N. Australia, ♀ 2; Queensland, ♂ type + 3, ♀ 1; Cape York, ♂ 2, ♀ 2; Port Denison, ♂ 1; Kuranda, ♂ 10, ♀ 2. Total ♂ 19, ♀ 8.

No. 102, *pyres*.

This well spotted species curiously lacks H.W. D.6 in the male, with the exception of the maximal specimen, and often in the female. Discal 8 on H.W. below, in the female allotype, is exceptional. On F.W. D.9-10 above are constant in the male but 9 is weaker in the female and absent from the minimal specimen. The female has little of the purple gloss of the male. The discals on the underside tend to become linear, and this is more noticeable in *mangolinella* (No. 103). A small and abnormal male from Florida looks very like *bismarckiana* (No. 108) on upper side, but is distinguished below by the discal streaks on H.W.

DISTRIBUTION. All forms of *pyres* are confined to the Solomon Islands: I have seen a record from "New Guinea", which is extremely doubtful.

"Solomon Isles", ♂ 24, ♀ 4; Choiseul, ♂ 2; Savo, ♀ type; Florida (with Tulagi), ♂ 13, ♀ 5; Guadalcanal, ♂ type + 55, ♀ 15. Total ♂ 95, ♀ 25.

No. 103, *mangolinella*.

This form has the spots larger, often much larger, tending to fuse together. The distribution is curiously patchy. Talbot (1916) remarks on its likeness to *Danaus melusina marcia* Talbot from Biak.

DISTRIBUTION. Bougainville, ♂ 6, ♀ type + 14; Ysabel, ♂ 6, ♀ 8; New Georgia, ♀ 1. Total ♂ 12, ♀ 24.

The unusual predominance of females in collections is probably due to the more striking appearance, the males being nearer to *pyres*. A record of the latter from Bougainville probably refers to a poorly marked *mangolinella*, for it will be noticed that these two are mutually exclusive.

No. 104, *paucinotata*.

A series of specimens in the Rothschild collection appears worthy of being distinguished by the poor development of the spots, even as compared with a

minimal *pyres*. The male always lacks D.6 on H.W. underside, like its female and also some females of *pyres*. A cell-spot is only shown in the maximal male, and is absent from the solitary female.

DISTRIBUTION. Choiseul, ♂ 1; Vella Lavella, ♂ type; Kolombangara, ♂ 2, ♀ 1. Total ♂ 4, ♀ 1. These three forms of *pyres* replace one another, save for the single ♂ *paucinotata* from Choiseul. It is curious that no form of *pyres* is known from Malaita or San Cristobal, which both have peculiar *Euploea* populations.

No. 105, *jamesi*.

Quite a distinct race. The F.W. submarginals violet tinted, often lacking from areas 1b-2, and considerably enlarged in 5-6. The maximal female, from Dampier Island, has H.W. exceptionally well-spotted above, with paired submarginals, and it also has as an exception a faint F.W. D.10 below. Butler's "*infantilis*" is merely a poorly spotted specimen.

DISTRIBUTION. Essentially a British New Guinea race. *Ex-German New Guinea*: Stefansort, ♂ 1; Finschhafen, ♂ 1; Dampier Island, ♂ 3, ♀ 2. *British New Guinea*: Hall Sound, ♂ type, ♀ type, and type ♂ "*infantilis*". From German border to Port Moresby and Yule Island, ♂ 74, ♀ 28. *Louisiade Archipelago*: Samarai, ♂ 1, ♀ 2; Doini Islet, ♂ 1; Sudest, ♂ 1. *D'Entrecasteaux Archipelago*: Goodenough, ♂ 4, ♀ 3; Fergusson, ♂ 2; Normanby, ♂ 1. Total ♂ 91, ♀ 36. A female from Yule Island or the neighbouring mainland, from the Bourke collection in the Hope Department, Oxford University Museum, is abnormal in having no spots above or below. Further knowledge may show this to be a local race.

No. 106, *phokion*.

Much blacker in ground-colour than *jamesi* with the submarginals more developed and, anteriorly at least, lilac in the male but all white in the female. On H.W. underside the admarginals are better developed. It is near to *jamesi* and occurs with it on Dampier Island.

DISTRIBUTION. *Ex-German New Guinea*, ♂ 28, ♀ 5 + ♂ neo-type; Stefansort, ♀ 1; Simbang, ♂ 2; Finschhafen ♀ neo-type; Huon Gulf, ♂ 3; Dampier Island, ♂ 5, ♀ 3; Sattelberg, ♂ 9. Total ♂ 48, ♀ 10.

No. 107, *salpinxoides*.

A light brown form, usually spotless above but sometimes with small lilac anterior submarginals. Very common in collections.

DISTRIBUTION. "*German New Guinea*", ♂ 10, ♀ 10; Vulcan Island, ♂ 4, ♀ 6; localities from Friedrichshaven to Sattelberg, ♂ 396, ♀ 40. Total ♂ 410, ♀ 56.

No. 108, *bismarckiana*.

The authorship of this race was erroneously ascribed by me in 1942 (p. 135) to Ribbe. A well-defined race with F.W. submarginals more uniform than in those previously considered, and a little blue suffusion only at the inner end of the large one in 6 in the male. Admarginals well developed on H.W. underside. The minimal specimen is from Rook Island, and others from that locality are poorly spotted and may be shown to be a distinct race when more specimens are available.

DISTRIBUTION. *Admiralty Islands*, ♂ 1. *Bismarck Archipelago*: Rook Island or Umboi, ♂ 3; New Britain, ♂ type + 51, ♀ type + 21; Duke of York Island, ♂ 18, ♀ 4; New Ireland, ♂ 10, ♀ 1; Queen Charlotte Island, ♂ 2. Total ♂ 86, ♀ 27. Two male specimens, collected by Ribbe in 1912 require confirmation. One, at Stockholm, is labelled "*Shortlands*", and a similar label is attached to one in Paris.

No. 109, *manusi*.

General coloration a darker purplish brown than in *bismarckiana*, and H.W. more strongly spotted. F.W. S.6 large as in *jamesi*; the series is more or less violet tinted on F.W., and white on H.W. The original description (Carpenter, 1942) needed minor amendments which have been made in the table.

DISTRIBUTION. *Admiralty Isles*: Manus, ♂ 10, ♀ 1.

No. 110, *nivani*.

The four specimens of this new race are very uniform; general coloration deep blackish brown. The submarginals on both wings very well developed, and clear white except for a minute blue edging at the proximal ends of 5-6.

DISTRIBUTION. *Louisiade Archipelago*: Nivani Island, ♂ 4, in Hope Department, University Museum, Oxford.

No. 111, *callithoe*.

This extremely variable, fine, species is very troublesome to deal with. I consider it here as divided under two headings, *callithoe* proper and *phaenareta*, the former adorned with bright blue, the latter dark and much less marked with spots and patches.

Some forms of *callithoe* occur in archipelagoes near New Guinea to its north and east. It has been impracticable to deal with some of them as "maximal" and "minimal" as it is impossible to say whether a certain specimen is the maximal of one form or the minimal of another. Females introduce another difficulty as it is not at present possible to assign certain forms to their proper males; often only one sex has been described as type. The forms which seem definite are, in particular, No. 113, *admiralia*, and, to a smaller degree, *eurykleia* and *arova*, Nos. 114 and 115.

The forms *callithoe*, No. 112A, *hansemanni*, No. 112B, *durrsteini* and the less spotted *nera* and *erynia* are an intergrading series. Several different forms may be found in one area and until more is known about them the nomenclature must remain very much a matter of opinion. There was much controversy between Honrath and Staudinger, and in 1895 Staudinger, after long discussion, admitted that he had begun to doubt some of his former statements. The forms *hansemanni* Honrath, 1888 and *durrsteini* Staudinger, 1890, mainly differ by the presence on F.W. in the former of well defined admarginals and submarginals, absent from the latter, and spots on H.W. in the former, absent from the latter. Since these spots are exceedingly variable much confusion has arisen. Both of these forms have the F.W. discals of *callithoe* enlarged and fused into a single patch. The "*biplagiata*" of Fruhstorfer, 1910, is merely a form of *callithoe* in which there are two large spots in the apex of the F.W. cell. But if the discal patch is reduced by the separate parts in each area appearing only at the base of the area, and only in part of the cell, the form *nera* Staudinger, 1895, is produced; if the spots are further reduced so as to be almost narrow streaks, the form *erynia* Fruhstorfer, 1912, results. The females range from quite dark forms with no spots or white areas on H.W., and F.W. with discrete and not very large discal spots, to specimens

of which the greater part of the centre of F.W. and most of H.W. are white or bluish white, with distinct admarginals and submarginals on F.W.

The following is an attempt to show how the forms are distributed among the specimens I have examined.

	<i>callithoe.</i>		<i>hansemanni.</i>		<i>durrsteini.</i>		<i>nera.</i>		<i>erynia.</i>	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>Dutch New Guinea</i>	1	1								
Arfak	18	1								
Geelvink Bay	12	1		3					2	2
Dorey	17	1								
"Salawatti"	2			5						
Humboldt Bay			1	5	8	3	1			2
<i>Ex-German New Guinea</i>			2	1	6	2	1			4
Vulcan I.			7	1		1				
? "Kapaur"	5	2								
Astrolabe Bay			1	5	4	4	8			9
Stephansort					4	2				3
Constantinehaven			4	1	6	2	2			
Sattelberg			1							
Finschhafen			5							
Simbang				2						
"Northern New Guinea"	2		+	1	+	1			1	1
<i>British New Guinea</i>										
"Mailu"	1									
Hydrographer Mts.	1									
Milne Bay	3	1								
Port Moresby				1						
<i>D'Entrecasteaux Archipelago</i>										
Goodenough I.	2									
	64	7	21	25	28	15	2	10	3	21
	71		46+		43+		12		24	
	<i>callithoe.</i>		<i>hansemanni.</i>		<i>durrsteini.</i>		<i>nera.</i>		<i>erynia.</i>	

No. 113, *admiralia*.

This race is more definite and easier to recognize than others that have been discussed. The spots are not so large, and the F.W. larger discals are separate in the male; the underside is more spotted than in the other forms, the admarginals being especially developed. The type female has the ground colour brownish black rather than the bluish black of the male; the spots are suffused with white, or almost white. The F.W. discals and submarginals meet; D.4-5-6 combine to form a patch. In the maximal male only in area 3 do discals and submarginals meet; D.4-6 are very large but not fused.

DISTRIBUTION. *Admiralty Isles*, ♂ 2; *Manus*, ♂ 7, ♀ 7. Total ♂ 9, ♀ 7. I have also had a report of ♂ 2 from *Los Negros* in the American Museum of Natural History.

No. 114, *eurykleia*.

Fortunately the types of this form described by Fruhstorfer have been available; it grades into *arova*. The male F.W. has, in the cell, anterior and posterior blue spots joined by a neck; a confluent blue patch is formed by the

more anterior discals. In the female this patch is whitish blue, including the cell, becoming bluer distally anterior to vein 2; H.W. admarginals and submarginals are bluish white.

DISTRIBUTION. *British New Guinea*: Milne Bay, ♂ 1. *Louisiade Archipelago*: Sudest, ♂ 8, ♀ 7 (often better spotted than elsewhere). *D'Entrecasteaux Archipelago*, ♂ 1; Goodenough, ♂ 7, ♀ 1; Fergusson, ♂ type +8, ♀ type +5. *Trobriand Archipelago*: Kiriwina, ♀ 1; Woodlark, ♂ 6, ♀ 2. Total ♂ 32, ♀ 17.

No. 115, *arova*.

The type differs from the type of *eurykleia* by the F.W. cell-spot being single and roughly circular. The anterior intra-cellular blue patch of *eurykleia* is, in *arova*, limited to a linear marking along the anterior border of the outer third of the cell. The blue markings have not the decidedly purplish tint of *eurykleia*. The underside is very feebly spotted.

DISTRIBUTION. *Louisiade Archipelago*: St. Aignan, ♂ 1, ♀ 1; Rossell, ♂ type +22, ♀ 6. *D'Entrecasteaux Archipelago*: Fergusson, ♂ 1. Total ♂ 25, ♀ 7. It will be noted that *eurykleia* and *arova* both occur on Fergusson, and in all probability should be merged under one name.

No. 116, *unibrunnea*.

This and the two following have none of the blue patches of *callithoe* forms and are very poorly spotted above. The maximal male is exceptional in having D.10 of F.W. represented below. In the maximal female a marginal white suffusion tends to obscure the spots on the upper side of H.W.; on the underside the submarginals are linked with discals by white streaks which are also seen in the maximal male in 1b and 1c. A.4 is always present on the F.W. underside. There are the following differences from *heurippa* on the underside: in *unibrunnea* the F.W. cell-spot is smaller, and D.4 and 10 may exceptionally be represented by traces; D.5-6 are absent. Some females (ab. *majuma* Ribbe, 1898), transitional to *browni*, have paler ground-colour, and whitish cell, and F.W. has faint dyslegnic whitish patches in the region of the submarginals and discals.

DISTRIBUTION. *Ex-German New Guinea*, ♀ 1. *Bismarck Archipelago*: New Britain, ♂ 6; Duke of York Island, ♂ type +1; New Ireland, ♂ 20, ♀ 7; Queen Charlotte Island, ♂ 4, ♀ 8; Feni, ♂ 5, ♀ 4. Total ♂ 37, ♀ 20.

No. 117, *browni*.

This strange white aberration has no spots above and only shows a few faintly below; the minimal male and female do not even show spots below.

DISTRIBUTION. *Bismarck Archipelago*: New Britain, ♂ 11, ♀ 22; New Ireland, ♂ 2; Duke of York Island, ♂ type +2, ♀ 1. Total ♂ 16, ♀ 23.

No. 118, *heurippa*.

A very dark race, but the maximally spotted specimens link it with *phaenareta phaenareta* Schaller, 1785. In the maximal male the F.W. discals tend to become streaks, and H.W. S.5-6 are lost in white suffusion. On the H.W. underside D.5-7 may have the shape of arrow-heads. In the maximal female white suffusion is strongly developed in F.W. areas 1b-4, and faintly in 5-7 and the end of the cell. On H.W. upper side D.5 may be prolonged to meet S.5, making a streak, and S.1b on the underside is prolonged into a streak. The almost invariable

presence on F.W. underside of A.4 in this subspecies and *unibrunnea* is remarkable ; it is exceptionally absent from minimal males.

Heurippa differs constantly from *unibrunnea* by not having F.W. D.10 on the underside, although this is not invariably present in *unibrunnea* ; on the upper side *unibrunnea* lacks D.9-10 which are generally present in *heurippa*.

DISTRIBUTION. "Solomons", ♂ 3 ; Bougainville, ♂ 6, ♀ 7 ; Fauro, ♂ 3, ♀ 2 ; Shortlands, ♂ 6 ; Alu, ♂ 6 ; Choiseul, ♂ 5, ♀ 3 ; Vella Lavella, ♂ 6, ♀ 2 ; Ganongga, ♂ 1, ♀ 1 ; Rubiana, ♂ 1, ♀ 4 ; Rendova, ♂ 2, ♀ 6 ; Ysabel, ♂ 5, ♀ 8 ; Florida (with Tulagi) ♂ 7, ♀ 8 ; Guadalcanal, ♂ type +39, ♀ type +11 ; Malaita, ♀ 1. Total ♂ 91, ♀ 54.

No. 119, *kadu*.

This is the only representative of the widely-spread *leucostictos* (*sensu stricto*) to be found in the area under discussion. The presence on F.W. underside of D.tr.3, and 4, is very unusual in the male ; in the female D.10 is smaller than in the male.

DISTRIBUTION. *Marianne Islands* : Guam, ♂ 97, ♀ 29 ; Saipan, ♂ 10, ♀ 7. Total ♂ 107, ♀ 36.

No. 120, *eustachius*.

This is the first of the many forms of *nemertes*, which has a huge area of distribution from the Moluccas through New Guinea eastwards to Fiji. Fruhstorfer ignores Kirby's description and his "*quintia*" is a synonym. He has, as with other polymorphic species, erected a number of named "races" some of which are so ill-defined, and so grading into others, that they cannot be considered valid.

Minimal males of *eustachius* are much the same as Fruhstorfer's *rhodia*. The characteristic of *eustachius* is enlargement of the anterior submarginals on F.W., and tinting with violet in the male. The type is blackish rather than reddish brown, and the proximal half of the large submarginal in 6 is violet. On the underside the submarginals are white on F.W., but some on H.W. may be blue. The maximal female is exceptionally well spotted. The type specimen of Fruhstorfer's "*quintia*" lacks D.10 on F.W. below which is well shown in *eustachius*, and "*quintia*" has admarginals in F.W. areas 1b, 2, 6, 7 on the underside.

DISTRIBUTION. *British New Guinea* : from the border to Milne Bay and Port Moresby, ♂ 47, ♀ 48. *Louisiade Archipelago* : Samarai, ♂ 1, ♀ 2 ; Nivani, ♂ 6, ♀ 2 ; Rossell, ♂ type +15, ♀ 12 ; Sudest, ♂ 10, ♀ 9 ; St. Aignan, ♂ 3, ♀ 7. *D'Entrecasteaux Archipelago*, ♂ 3, ♀ 1 ; Fergusson, ♂ 31, ♀ 3 ; Goodenough, ♂ 22, ♀ 17. *New Hebrides*, ♂ 2, ♀ 1. Total ♂ 141, ♀ 102. Some specimens of No. 133, *iphianassa*, from Torres Isles differ little from *eustachius* except by their somewhat more developed D.10 on F.W. above. The anterior submarginals may be almost as large and as violet tinted as in normal *eustachius*, but in this the more posterior submarginals are better developed.

No. 121, *aviena*.

Fruhstorfer's description of this, from Finschhafen, scarcely separates it from *eustachius*. But on the whole it seems that specimens from ex-German territory can be separated by the F.W. submarginals in 6,7,8 not being so much larger than the others. A long series from ex-German New Guinea, however, does not consistently show very dark ground-colour ; some males from Simbang are quite

light brown, others like the darker specimens which Fruhstorfer calls "*quintia*". This form undoubtedly grades into *eustachius*.

DISTRIBUTION. *Ex-German New Guinea*, ♂ 19 +2 trans. to *eustachius*, ♀ 8 +1 trans. to *eustachius*; Dampier Island, ♂ 7, ♀ 5. *British New Guinea*: between Holnicote Bay and border, ♂ 7, ♀ 1; Milne Bay, ♂ 1. *Louisiade Archipelago*: Rossell Island, ♂ 1. Total, ♂ 35 +2 transitional, ♀ 14 +1 transitional.

No. 122, *erima*.

This light coloured form must include *gorima* and *atomaria* of Fruhstorfer (1910); both poorly spotted.

DISTRIBUTION. *Ex-German New Guinea*, ♂ 113, ♀ 12, +types; Vulcan Island, ♂ 4; Dampier Island, ♀ 1. Total ♂ 118, ♀ 14.

No. 123, *rhodia*.

No types available. The description by Fruhstorfer (1910) implies no large spots at all on F.W. Under this name I include a number of very poorly spotted specimens, chiefly from the Trobriand Islands, some of which are very like a series of Ribbe's "*ulaguna*" (*perdita*) in the Rothschild collection. But *perdita* has the brand so uniformly smaller than in *rhodia* that the latter can be separated. Quite spotless specimens resemble *polymela* (No. 128) but that has a brand of bluer tint than that of *rhodia* which is browner. The females of *rhodia* vary in colour from a dark blackish brown with almost a purple tinge to a brown as pale as in some *perdita*.

DISTRIBUTION. *British New Guinea*: Milne Bay, ♂ 1; Yule Island, ♂ 1. *D'Entrecasteaux Archipelago*: Fergusson, ♂ 5, ♀ 2. *Trobriand Archipelago*: Kiriwina, ♂ 11, ♀ 4; Woodlark, ♂ 10, ♀ 4. Total ♂ 28, ♀ 10.

No. 124, *messia*.

Fruhstorfer's inadequate description says this form is like *rhodia* but smaller; "above with much larger milk-white discal spots on fore-wing"; the locality was given as Woodlark Island.

G. Talbot made the following comment in a note attached to a female specimen in the British Museum. "The only specimen in Fruhstorfer's collection. Sex not stated in Fruhstorfer's description, but should have large white discal spots on *upper* side. The *under* side is probably meant." The specimen, selected as lectotype, is small and poorly spotted. On the F.W. *under* side D.2 is large and round, and 10 also is well developed.

DISTRIBUTION. *Trobriand Archipelago*: Woodlark Island, ♀ 1.

No. 125, *affinita*.

Under this name Rothschild's *nemertoides* (1915) from Manus can be sunk. F.W. D.10 is always present, and D.9 is present in maximal specimens as a streak on the underside. D.1b on the upper side is large and may have the posterior portion broken off as an accessory; in the maximal female the spot is deeply notched externally. The H.W. submarginals 2-3, when present on the underside of the male are blue, the remaining spots clear white.

DISTRIBUTION. "*Admiralty Isles*", ♂ 2, ♀ type; Manus, ♂ 10, ♀ 7; Los Negros, ♂ 4, ♀ 2; Pak or St. Gabriel, ♂ 3. Total ♂ 19, ♀ 10.

No. 126, *perdita*.

A small form, rather red- than yellow-brown, with small spots. I can see no adequate reason for separating Ribbe's "*ulaguna*" which can be sunk as a synonym. F.W. D.10 is only shown in maximal specimens on the upper side, and D.3 above only on the maximal female, although the maximal male shows it below. The submarginals on H.W. underside are usually blue tinted in the male.

DISTRIBUTION. *Bismarck Archipelago*, ♂ 1; Rook Island or Umboi, ♂ 6, ♀ 7; New Britain, ♂ 49, ♀ 27; Duke of York Island, ♂ type +9, ♀ type +6; New Ireland, ♂ 12, ♀ 3; Queen Charlotte Island, ♂ 9, ♀ 6; Feni, ♂ 5, ♀ 1. Total ♂ 92, ♀ 51.

A specimen in the Rothschild collection labelled "New Georgia", collected by Webster, must be regarded as suspect.

No. 127, *pulchella*.

This, the smallest of all forms of *nemertes*, is easily known by the grey tint towards the apex of F.W.; this feature distinguishes also the subspecies *griseitincta* of *cerberus* (No. 21) and *mathiasana* of *illudens* (No. 48).

DISTRIBUTION. *Bismarck Archipelago*: St. Mathias Island, ♂ type +18, ♀ type +3; Squally Island, ♂ 4, ♀ 3 (slightly different, seeming transitional between *pulchella* and *perdita*). Total ♂ 23, ♀ 7.

No. 128, *polymela*.

This common subspecies seems to have two strains, one lighter, so that the yellowish-brown male is almost as light as some *erima*; the other very dark, almost black; and they intermingle. The race *bernsteinii* C. & R. Felder, 1865, of the Moluccas, much resembles some specimens of *polymela*, but the latter has the sex mark on F.W. oval and purple tinted whereas in *bernsteinii* it is smaller, circular, and more yellowish in colour. Generally, the admarginals are poorly developed beneath, and F.W. submarginals only show above in the females. The presence of F.W. D.10 above and of D.9 and D.11 beneath is exceptional.

DISTRIBUTION. *Trobriand Archipelago*: Yanaba (Egum group), ♀ 6. *Solomons*: Nissan ♂ 6; Bougainville, ♂ 9, ♀ 7; Ovan, ♂ 1; Fauro, ♂ 1, ♀ 6; Shortlands, ♂ 5, ♀ 1; Alu, ♂ type +7, ♀ type +10; Treasury, ♂ 3, ♀ 1; Vella Lavella, ♂ 10, ♀ 7; Bava or Bagga, ♂ 1; Ganongga, ♂ 1, ♀ 4; Gizo, ♂ 3; Kolombangara, ♂ 3, ♀ 4; New Georgia, ♀ 6; Rubiana, ♂ 4, ♀ 6; Rendova, ♂ 3, ♀ 7; Ysabel, ♂ 5, ♀ 7; "Islets near Ysabel", ♀ 3; Huleo Islet, ♂ 10; Russell Isles, ♂ 10, ♀ 4; Savo, ♂ 1, ♀ 2; Nangatana, ♂ 1; Florida, ♂ 12, ♀ 3; Tulagi, ♂ 23, ♀ 13; Guadalcanal, ♂ 31, ♀ 24; Malaita, ♂ 6, ♀ 11; Ulawa, ♂ 3. *Santa Cruz*, ♂ 1. Total ♂ 162, ♀ 133.

The wide distribution of *polymela* throughout the Solomons, extending even to the extreme north, Nissan, and to one island in the Trobriand group, makes more remarkable its apparent absence from Choiseul, and San Cristobal and its associates, especially as it is present on Ulawa. The specimen from Santa Cruz, taken by R. A. Lever, is of particular interest, seeing that another form of *nemertes* occurs there: possibly this one was an intruder.

No. 129, *imitata*.

This white-bordered form was originally considered to be a separate species; it is remarkably like *assimilata* C. & R. Felder, 1865, from the Aru and Kei Islands, but small differences can be seen. The submarginals on the H.W. underside of *assimilata*, and a discal 7, are often large and blue tinted, but in *imitata* are very small. There are radial streaks on the H.W. of *imitata*, each commencing at a dot on the edge of the wing and running inwards along the middle of each

area (though not always shown in all areas) as far as the submarginal level ; these are not seen in *assimilata*. The outline of the basal brown in both wings is different in the two forms ; in *imitata* the brown is replaced to a greater extent by white around the end of the cell, giving the brown an angular outline which is not seen in *assimilata* where the brown is more smoothly rounded. On the F.W. upper side *imitata* always shows D.10 but in *assimilata* area 10 is filled with white which also may invade area 11. On the underside of the F.W. of *assimilata* the brown comes much nearer to the edge of the wing in area 1b than elsewhere, which is not so in *imitata*.

DISTRIBUTION. "Solomons", ♂ type ; San Cristobal, ♂ 7, ♀ 3 ; Santa Ana, ♂ 10, ♀ 2 ; Ugi, ♀ 5. Total ♂ 18, ♀ 10.

No. 130, *rossi*.

Named as a compliment to Dr. E. S. Ross, of the California Academy of Sciences, in acknowledgement of his kindness in sending me for study the valuable *Euploea* collected by the Templeton-Crocker expedition of 1933 on Rennell Island and elsewhere.

This unique specimen has the row of submarginals on H.W. more uniform in size than is usual in forms of *nemertes*, but 6 is still the largest ; 1b is blended with the admarginals. The submarginals are white with bluish margins in 2-9. The brand is narrow antero-posteriorly, and more like that of a *leucostictos* than a *nemertes* form ; it is slightly blue and measures $4\frac{1}{2}$ mm. transversely by $1\frac{1}{2}$ mm. antero-posteriorly. The paired admarginals of H.W. are linked to the submarginals and the compound patch in each area 1c-3 is H-shaped from prolongation at the corners. The underside of F.W. has D.2 bluer than the submarginal series, and D.10 is clearly shown. The ground colour is Ridgway's "Aniline-black" above, slightly lighter below.

DISTRIBUTION. *Solomons Islands* : Rennell, ♂ holotype, in California Academy of Sciences. (See addendum (p. 158) for further specimens.)

No. 131, *crucis*.

This new subspecies is smaller than the average *polymela*, and about the size of *novarum-ebudum*. The general coloration is comparable with that of *hisme* and *herbstii*, Boisduval, 1832 ; it is a rich brown with darker discal area on F.W. and lighter H.W. anal area. The underside is much paler than that of *herbstii*, which is almost black. The H.W. submarginals of *crucis* are scarcely blued, while in *herbstii* they are strongly blued, and better developed. The F.W. brand differs from that of both *herbstii* and *hisme* ; it is more elongated, oval, and tinted brown whereas in *herbstii* it is smaller, more circular and tinted blue ; in *hisme* also smaller and bluish. Both *crucis* and *herbstii* may show traces of submarginals on F.W. apex. The female allotype of *crucis* is much like a *novarum-ebudum* in which the spots are poorly developed.

DISTRIBUTION. "Santa Cruz Islands", ♂ paratype and ♀ allotype : Santa Cruz Island, ♂ holotype and paratype. The holotype is in the American Museum of Natural History, the other specimens at Oxford, collected by R. A. Lever. Total ♂ 3, ♀ 1. The small *polymela*, collected by Lever, has already been noted under that name.

No. 132, *eustachiella*.

The name of this new form suggests likeness to small *eustachius*. The male holotype has an expanse of 60 mm., the allotype 64 mm., the female paratype 66 mm. Of fourteen male *eustachius* the smallest has an expanse of 62 mm., the others range up to 75 mm.; of five females the smallest measures 65, the largest 67 mm.

Male type: discal area of F.W. dark brown, but not so blackish as in *eustachius*; on H.W. only the cell is of the dark shade. F.W. submarginals 4-5 are small, 6-7 larger and bluish, 8 bluish; on H.W. underside S.4-6 are bluish. The female allotype has F.W. S.4-5 small, 6-8 larger and bluish. On comparison with many *eustachius* none of them showed such a contrast between the large F.W. 6-7 and the smaller size or absence, in area 2 as do both the *eustachiella*.

All three specimens from the Templeton-Crocker expedition. Male type and allotype in California Academy of Sciences, female paratype at Oxford, collected by M. Willows, Jr., 15 July, 1933.

DISTRIBUTION. *Santa Cruz Isles*: Anuta or Cherry Isle, ♂ holotype, ♀ allotype + 1.

No. 133, *iphianassa*.

A variable race of large size, differing from *eustachius* by the small size of the anterior submarginals, which are not noticeably tinted blue. It grades on the one hand into *eustachius* and on the other into *novarum-ebudum*. Poorly spotted specimens, to which Butler in 1878 gave the name *consanguinea* which is now sunk as a synonym, may resemble *perdita*. The (slight) enlargement of the anterior F.W. submarginals distinguishes *iphianassa* from *macleayi* in which they agree more in size with the posterior spots.

DISTRIBUTION. *Santa Cruz Isles*: Tikopia, ♂ 5. *Torres Isles*: Hiw, ♂ 8; Loh, ♂ 1; Tegua, ♂ 2, ♀ 2.

"*New Hebrides*", ♂ 4, ♀ 9: Espiritu Santo, ♂ 1; Malekula, ♀ 1; Tana, ♂ 18, ♀ 2; Aneityum, ♂ ♀ types *iphianassa*, ♂ ♀ types *consanguinea*. *New Caledonia*: Noumea, ♂ 1. Total ♂ 42, ♀ 16.

A female in the National Collection labelled "*Queensland*" must be looked upon as suspect.

No. 134, *novarum-ebudum*.

Formerly, incorrectly, known as "*graeffiana*" (Carpenter, 1942). A small race, with F.W. submarginals more or less equal in size and those on H.W. well developed, especially in the female. Both wings have paler borders beyond the submarginals. F.W. D.10 well shown above. Admarginals are absent even on underside of H.W. There is a tendency in the females for the submarginals to become so diffuse that they may almost make a white border, but the origin of this is always quite obvious.

This race merges into *macleayi* if the paler border is less pronounced; and also merges into *iphianassa*.

DISTRIBUTION. *Santa Cruz Isles*: Tikopia, ♂ 1 (trans. to *iphianassa*). *Banks Islands*: Reef Island, ♂ 1; Valua, ♂ 2; Vanua Lava, ♀ 2; Gaua, ♂ 6, ♀ 2. *New Hebrides*: Espiritu Santo, ♂ 12, ♀ 11; Aore, ♀ 1; Malo, ♂ 2; Aoba, ♂ 2, ♀ 3; Pentecost, ♂ 7, ♀ 7; Ambrim, ♀ 1; Malekula, ♂ 3, ♀ 4; Epi, ♂ 38, ♀ 7; Efate, ♂ 2, ♀ 4; Tana, ♀ 1. *Fiji*: Koro, ♂ 1 (*N.B.* at same time and place as a typical *macleayi*). Total ♂ 77, ♀ 43.

No. 135, *macleayi*.

Closely related to the last two races. It may be distinguished from *iphianassa* by F.W. submarginals forming a more complete series posteriorly, and from

novarum-ebudum by its larger size and less pale border. F.W. D.10 is always present above; there may occasionally be admarginals on H.W. underside. Some of the females are very close to *novarum-ebudum* and a specimen from Ovalau has carried still further the development of the white border. All the submarginals are much enlarged and most of them have become dyslegnic white patches, especially at the apex of F.W. and anal half of H.W. But the brown veins prevent the continuity which would make a complete white border. Two females from Lakemba (Pl. 9, fig. 4) have carried the process further so that there is a likeness to *imitata*. The F.W. shows no separate spots, and from area 10, all round the wing to the tornus there is a white border slightly dusted with brown at the edge of the wing and in area 1a. The inner margin of this is dentate. The same border is shown on H.W., but submarginals are visible along its inner edge, as pairs in 2-3, single and better defined in 4,5,6. On underside of F.W. submarginals can be faintly seen in 2-3, and D.2 is clear white. The H.W. shows submarginals more clearly on the underside, with an additional 7.

DISTRIBUTION. "Fiji", ♂ 14, ♀ type +13: Viti Levu, ♂ 6, ♀ 3; Bega or Mbengha, ♂ 3, ♀ 2; Ovalau, ♂ 11, ♀ 14; Nasova, ♂ 1; Vanua Levu, ♀ 1; Taveuni, ♂ 1, ♀ 1; Koro, ♂ 4, ♀ 1; Kandavu, ♂ 4, ♀ 7; Ono, ♂ 6; Totoya, ♂ 1, ♀ 2; Moala, ♂ 2, ♀ 2; Lakemba, ♂ 3, ♀ 3; Thithia, ♀ 5; Mango, ♂ 3, ♀ 1; Vanua Mbalavu, ♂ 4, ♀ 13; Naitamba, ♂ 1. Total ♂ 64, ♀ 69.

No. 136, *usipetes*.

The nomino-typical form is spotless above and below, with a buff patch on F.W. The maximal specimens show some minute submarginals.

DISTRIBUTION. *Aru Islands*, ♂ 25, ♀ 9. *New Guinea*: Port Moresby, ♂ type +1; Ekeikei, ♂ 1; Yule Island, ♀ 1. Total ♂ 28, ♀ 10.

Waterhouse & Lyell (1914) figure the type of *hippias* Miskin, 1890, from Cape York, and refer to one other specimen, a female, from Thursday Island, and say these "are the only Australian examples known". I have compared the figure with the type specimens of *usipetes usipetes* in the British Museum (Nat. Hist.) and there is no doubt that *hippias* is *usipetes*.

No. 137, *rezia*.

Differs from *usipetes* by the presence of F.W. submarginals. The maximal male has D.10 on F.W., which is exceptional. If the F.W. buff area is whitish distally, the form *astrifera*, and if mostly white, the form *albodiscalis* of Fruhstorfer, 1910, are produced.

DISTRIBUTION. "New Guinea", ♀ 1. "Dutch New Guinea", ♀ type *astrifera*. *Ex-German New Guinea*: Constantinehaven, ♂ 1; Vulcan Island, ♂ 1, ♀ 1. *British New Guinea*: from border to Milne Bay, Port Moresby and Yule Island, ♂ 53, ♀ 50. *Louisiade Archipelago*: Samarai, ♂ type +1, ♀ type +3; Doini Islet, ♀ 1; Sariba Islet, ♂ 1. *D'Entrecasteaux Archipelago*: Goodenough, ♂ 1; Fergusson, ♀ type *albodiscalis* +1. Total ♂ 59, ♀ 60.

PART 4. FAUNISTIC.

The general distribution of the genus *Euploea* is given by Hulstaert (1931, *Gen. Insect.*, Fasc. 193: 98). Abundant in tropics, but not entering the palaearctic region. Characteristic of the Indo-Australian fauna, from the Indian peninsula to the Pacific Islands and Australia, and into southern China and the Riu-Kiu Islands. Westwards it enters the Ethiopian region but only the small Mascarene Islands

of the Indian Ocean, not reaching Madagascar or the African continent. An unfortunate slip by Talbot (1947, p. 2) gives "Madagascar and the neighbouring islands" instead of "Mascarene" Islands. The genus is well represented in the Seychelles. Fruhstorfer (1910) says "Starting from two centres of distribution, continental India and New Guinea, the number of species rapidly decreases on the remote island groups. Northwards they are still numerous on Formosa, but on the Loo-Choo Islands they become extremely rare". I have been unable to find, from recent books on the butterflies of India, any indication of the western limit of distribution. One of the most beautiful species *algea deione* Westwood, 1848, is found in Sikkim, Tibet and Afghanistan.

According to the character of their *Euploea* fauna the islands in the area selected for this study can be grouped as follows :—

I. BISMARCKIAN.

- (A) Admiralty Islands.
- (B) Bismarck Archipelago.

II. PAPUASIAN.

- (A) Vulcan Island.
- (B) Dampier Island.
- (C) Louisiade Archipelago, including (as a result of this study) Rennell Island which geographically and politically is classed as one of the Solomon Island Group.
- (D) D'Entrecasteaux Islands.
- (E) Trobriand Islands.

III. SOLOMONS.

- (A) Solomon Islands.
- (B) Santa Cruz Islands.

IV. NEW HEBRIDESIAN.

- (A) Torres Islands.
- (B) Banks Islands.
- (C) New Hebrides.

V. NEW CALEDONIAN.

- (A) New Caledonia and Île des Pins.
- (B) Loyalties.

VI. AUSTRALIAN.

VII. FIJIAN.

- (A) Fiji, with Wallis Isle and Ellice Group.
- (B) Tonga or Friendly Isles.
- (C) Niue.
- (D) Samoa or Navigators Islands.
- (E) Union Island or Tokelau.
- (F) Cook or Savage Islands.
- (G) Tahiti or Society Islands.

VIII. NORTH PACIFIC (MICRONESIA)

- (A) Palau.
- (B) Marianne Islands

The Bismarckian Area.

(A) *Admiralty Isles*. In all areas the islands are taken from west to east. Under each section the serial number of a form will only be given on first mention.

(1) Marengan or D'Entrecasteaux Islet : No. 85, *ursula*, ♂6, ♀3. Total 9.

(2) Manus : No. 11, *doretta* (record only) ; No. 13, *nobilis*, ♂4 ; No. 18, *insulicola*, ♂3, ♀10 ; No. 46, *subnobilis*, ♂1, ♀1 ; *ursula*, ♂4, ♀4 ; No. 109, *manusi*, ♂10, ♀1 ; No. 113, *admiralia*, ♂7, ♀7 ; No. 125, *affinita*, ♂7, ♀7. Total ♂36, ♀30.

(3) Los Negros : *doretta* (record only) ; *nobilis*, ♂2 ; *ursula*, ♂5, ♀5 ; *admiralia* (record only) ; *affinita*, ♂4, ♀2. Total ♂11, ♀7.

(4) St. Gabriel, or Pak : *affinita*, ♂3. Total ♂3.

(B) *Bismarck Archipelago*. "Bismarcks", No. 126, *perdita* ♂1.

(1) Long Island : According to the map this island seems to be one end of the curving line which at the other extreme is completed by New Hanover, or Queen Charlotte Island. On the other hand it lies so close to Papua that it might have to be included with Vulcan and Dampier Islands in the next section. It is a lamentable fact that I have not been able to find a single *Euploea* from Long Island.

(2) Rook Island or Umboi : No. 19, *cerberus*, ♂3, ♀3 ; No. 45, *umboina*, ♂1 ; No. 47, *illudens*, ♂6, ♀1 ; No. 108, *bismarckiana*, ♂3 ; No. 126, *perdita*, ♂6, ♀7. Total ♂19, ♀11. According to Rothschild and Hartert (1914) "the ornis is that of New Britain".

(3) Witu or French Island : No. 90, *jessica*, ♂13, ♀15. Total ♂13, ♀15.

(4) New Britain : *doretta*, ♂17 ; *cerberus*, ♂26, ♀10 ; No. 22, *obscura*, ♂13, ♀2 ; No. 23, *eboraci*, ♂3, ♀4 ; No. 42, *lacon*, ♂4, ♀2 ; *illudens*, ♂43, ♀21 ; No. 86, *gaedei*, ♀1 ; No. 87, *caerulescens*, ♂28, ♀23 ; *jessica*, ♂9, ♀1 ; *bismarckiana*, ♂52, ♀22 ; No. 116, *unibrunnea*, ♂6 ; No. 117, *browni*, ♂11, ♀22 ; *perdita*, ♂49, ♀27. Total ♂261, ♀135.

(5) Duke of York Island : *doretta*, ♂2, ♀2 ; *cerberus*, ♂1, ♀1 ; *obscura*, ♂6, ♀1 ; *eboraci*, ♂4, ♀1 ; *lacon*, ♂1 ; *illudens*, ♂17, ♀9 ; No. 82, *treitschkei*, ♂4, ♀2 ; *ursula*, ♂1, ♀2 ; *caerulescens*, ♂3, ♀5 ; *bismarckiana*, ♂18, ♀4 ; *unibrunnea*, ♂2 ; *browni*, ♂3, ♀1 ; *perdita*, ♂10, ♀7. Total ♂72, ♀35.

(6) New Ireland : *doretta*, ♂3 ; *cerberus*, ♂4 ; No. 20, *subpunctata*, ♂2, ♀5 ; *obscura*, ♂1 ; No. 26, *auritincta*, ♂4 ; *illudens*, ♂24, ♀4 ; *treitschkei*, ♂8, ♀9 ; *ursula*, ♂3 ; *gaedei*, ♀1 ; No. 89, *viridis*, ♀2 ; *jessica*, ♂25, ♀21 ; *bismarckiana*, ♂10, ♀1 ; *unibrunnea*, ♂20, ♀7 ; *browni*, ♂2 ; *perdita*, ♂12, ♀3. Total ♂118, ♀33.

(7) Queen Charlotte Isle : *doretta*, ♂4 ; *cerberus*, ♂1 ; *obscura*, ♂1 ; *illudens*, ♂8, ♀3 ; *treitschkei*, ♂9, ♀4 ; *caerulescens*, ♂9, ♀4 ; *bismarckiana*, ♂2 ; *unibrunnea*, ♂4, ♀8 ; *perdita*, ♂9, ♀6. Total ♂47, ♀25.

(8) St. Mathias Island : No. 21, *griseitincta*, ♂6, ♀1 ; No. 48, *mathiasana*, ♂15, ♀5 ; *ursula*, ♂4, ♀4 ; No. 88, *eulegnica*, ♂7, ♀7 ; No. 127, *pulchella*, ♂19, ♀4. Total ♂51, ♀21.

(9) Squally Island or Emirau : *illudens*, ♂1 ; *ursula*, ♂2, ♀2 ; *eulegnica*, ♂2, ♀2 ; *pulchella*, ♂4, ♀3. Total ♂9, ♀7.

(10) Feni Island : *doretta*, ♂6 ; *cerberus*, ♂2, ♀2 ; *illudens*, ♂5, ♀2 ; *treitschkei*, ♂8, ♀10 ; *jessica*, ♀2 ; *unibrunnea*, ♂5, ♀4 ; *perdita*, ♂5, ♀1. Total ♂31, ♀21.

It is clear from the data that while the Bismarcks and Admiralty groups have certain features in common they are separable by others. Both have derived their fauna from New Guinea but lack certain species of that area, *e.g.*, forms of *batesii* (except for No. 26 on New Ireland) and *alcathoe*, and the whole of the complexes of *algea* and *sylvester*. On the other hand, Bismarckia is the only part of our whole area in which forms of *climena* (except for No. 12) and *modesta* and its allies, are represented. The differences between the Admiralties and the Bismarcks in the representation of *phaenareta* and *nemertes* are noteworthy, and it should also be noted that St. Mathias has three forms peculiar to it, *griseitincta*, *mathiasana* and *pulchella*. Hartert (1924) says that zoo-geographically St. Mathias is obviously nearest to "New Hanover" but there is a very interesting affinity in certain cases to the Admiralty Isles or Manus. The number of peculiar forms is great. Cheesman (1951) has some interesting remarks on the old geanticline, never entirely submerged, which comprised South West New Britain and the northern coast of New Guinea.

The tabular statement (p. 128) shows that the Admiralties, out of the total of eight forms, share only two (*doretta* and *ursula*) with the Bismarcks, but that the Bismarcks have many that are absent from the Admiralties. The number of forms of *treitschkei* on the Bismarcks contrasts with the single form on the Admiralties, also present on the Bismarcks. Nissan Island which is geographically and administratively included in the Solomons (q.v., *infra*) is an interesting link between these two areas. The presence of *polymela* speaks of affinity with the Solomons, but it is curious that *fraudulenta*, that other feature of the Solomons fauna, has not been recorded from Nissan. On the other hand there are on Nissan, and no other island of the Solomons group, two forms belonging to the Bismarckian area, *illudens* and *eulegnica*.

The Papuan Area.

The various islands near the coast of Papua have only been considered if they have furnished forms obviously derived from New Guinea and leading to those of the archipelagoes considered in this area. Thus, although Yule Island off the south coast of Papua has interesting features, they are only concerned with the mainland of New Guinea.

On the other hand, Vulcan Island (or Manam) and Dampier Island (or Karkar) appeared on the map to be so much in line with the curve of Bismarckia that they are considered, but their fauna has not much in common with that of the Bismarck Archipelago, being chiefly Papuan.

(A) *Vulcan Island*. No. 16, *weneri*, ♂7, ♀6; No. 83, *eugenia*, ♂5, ♀7; No. 95, *dudgeonis*, ♂1, ♀1; No. 107, *salpinxoides*, ♂4, ♀6; No. 112A, *hansemanni*, ♂7, ♀1; No. 112B, *durrsteini*, ♀1; No. 122, *erima*, ♂4, ♀4; No. 137, *rezia*, ♂1, ♀1. Total ♂29, ♀27.

(B) *Dampier Island*. No. 15, *misagenes*, ♂6, ♀6; No. 36, *coffea*, ♂3; No. 84, *dampierensis*, ♂4, ♀2; No. 105, *jamesi*, ♂3, ♀2; No. 106, *phokion*, ♂5, ♀3; No. 121, *aviena*, ♀1; No. 122, *erima*, ♀1. Total ♂28, ♀19. Rothschild (1915) recorded one *salpinxoides* from Dampier but this has not been found in the collections by myself or Mr. G. E. Tite to whom I wrote for confirmation; it was almost

	D'Entrecasteaux	Manus	Los Negros	St. Gabriel	Rook I.	Witu	N. Britain	D. of York I.	N. Ireland	Q. Charlotte I.	St. Mathias	Squally I.	Feni
11, <i>doretta</i>		+	+				+	+	+	+			+
13, <i>nobilis</i>		+	+										
18, <i>insulicola</i>		+											
19, <i>cerberus</i>					+		+	+	+	+			+
20, <i>subpunctata</i>									+				
21, <i>griseitincta</i>											+		
22, <i>obscura</i>							+	+	+	+			
23, <i>eboraci</i>							+	+					
26, <i>auritincta</i>									+				
42, <i>lacon</i>							+	+					
45, <i>umboina</i>					+								
46, <i>subnobilis</i>		+											
47, <i>illudens</i>					+		+	+	+	+		+	+
48, <i>mathiasana</i>											+		
82, <i>treitschkei</i>								+	+	+			+
85, <i>ursula</i>	+	+	+					+	+	+	+	+	
86, <i>gaedei</i>							+		+				
87, <i>caerulescens</i>							+	+		+			
88, <i>eulegnica</i>											+	+	
89, <i>viridis</i>									+				
90, <i>jessica</i>						+	+		+				+
108, <i>bismarckiana</i>					+		+	+	+	+			
109, <i>manusi</i>		+											
113, <i>admiralia</i>		+	+										
116, <i>umbrunnea</i>							+	+	+	+			+
117, <i>browni</i>							+	+	+				
125, <i>affinita</i>		+	+	+					+				
126, <i>perdita</i>					+		+	+		+			+
127, <i>pulchella</i>											+	+	

certainly an error and should have been recorded with the others for Vulcan. This makes all the more striking the contrast between these two islands lying in such similar relation to the coast of Papua; there can have been no connection between the two of them, or between them and the Bismarck Archipelago. One female of *erima* is the only coincidence between Dampier and Vulcan Island.

Some reference to a recent publication by Cheesman (1951) may be made here. She points out that New Guinea was raised from a drowned land mass by the Miocene-Pliocene tectonic movements. Since the only subsequent continental connections were periodical, with Queensland and by bridges to Asia through the Philippines (see later, *leucostictos*, p. 144) New Guinea might be expected to have a fauna basically Australian with an Oriental influence. This is emphatically not the case with *Euploea*, but precisely the opposite. Cheesman also points out that "genera which are represented in both *Malaysia* and *Papuasias* are also found in India, Burma or China . . .". Within the great genus *Euploea* itself, divided by the late A. S. Corbet into eleven groups, three of these groups, containing the familiar glossy blue males of *mulciber*, are not found in the area under consideration: possibly they were only evolved after the connections between Malaysia and Papuasias had broken down. The typical species of the *midanus*

group, well known by their glossy blue males, do not occur in our area, in which the group is represented only by the *leucostictos* complex.

(C) *The Louisiade Archipelago*. This is defined in the "Pacific Islands Pilot", 1921, Vol. 1, as "including the islands comprised within the parallels of 10° 10' S. and 11° 50' S. and the meridians of 150° 55' E. and 154° 30' E.; it is part of the territory of Papua". The important island, Samarai, or Dinner Island, not coming within these limits, is included for the purposes of this study.

A surprising discovery has been that Rennell, one of the Solomon Islands administratively and geographically, has been found to be faunistically more closely associated with New Guinea and is accordingly included in the Papuan area. This result is derived from the only known collection from that island and may of course be altered when more knowledge is available.

(1) Samarai, or Dinner Island: No. 39, *samaraina*, ♂1; No. 73, *eurianassa*, ♂1, ♀1; No. 89, *viridis*, ♂3, ♀4; No. 105, *jamesi*, ♂1, ♀2; No. 120, *eustachius*, ♂1, ♀2; No. 137, *rezia*, ♂2, ♀4. Total ♂9, ♀13. Sundry small islets near Samarai have furnished no other forms.

(2) Conflict Island, between Samarai and St. Aignan, 10° 45' S., 151° 44' E.: No. 29, *rotunda*, ♀1; No. 31, *resarta*, ♀1. Total ♀2.

(3) Nivani Island, 10° 48' S., 152° 23' E., a little south of the Deboyne group: *resarta*, ♂3; *eurianassa*, ♂5; *viridis*, ♀2; No. 91, *aenea*, ♂1; No. 110, *nivani*, ♂4; *eustachius*, ♂6, ♀2. Total ♂19, ♀4.

(4) St. Aignan, or Misima: *resarta*, ♂1; *eurianassa*, ♂4, ♀2; No. 85, *ursula*, ♂1, ♀1; *viridis*, ♀2; No. 90, *jessica*, ♂6, ♀3; *eustachius*, ♂3, ♀7. Total ♂15, ♀15.

(5) Sudest, or Tagula: *resarta*, ♂3; *eurianassa*, ♂23, ♀2; *jessica*, ♂5, ♀8; *jamesi*, ♂1; No. 114, *eurykleia*, ♂8, ♀7; *eustachius*, ♂10, ♀9. Total ♂50, ♀26.

(6) Rossell, or Yela: *eurianassa*, ♂28, ♀2; *ursula*, ♂2, ♀1; *jessica*, ♂9, ♀5; No. 115, *arova*, ♂13, ♀6; *eustachius*, ♂16, ♀12; No. 121, *aviena*, ♂1. Total ♂69, ♀26.

It will be convenient to discuss these six before going on to consider Rennell. The following typically Papuan forms are almost universal on these islands, *resarta*, *eurianassa*, *eustachius*; the *viridis* and *jessica* forms of *treitschkei* occur on three, though only St. Aignan has produced both. Samarai, the nearest to Papua, possesses a unique form (Pl. 4, fig. 1) belonging to the *alcathoe* group, which has not been seen from any of the other islands. The presence of *jamesi* on Samarai and Sudest speaks strongly of the Papuan character of the Louisiade fauna. (See tabular statement on page 130.)

(7) Rennell Island: No. 32, *kunggana*, ♂2, ♀3; No. 60, *fraudulenta*, ♂2; No. 62, *brenchleyi*, ♂1; No. 44, *rennellsensis*, ♂26; No. 130, *rossi*, ♂1. Total ♂32, ♀3. Three of these are new to science (Pl. 5) and confined to Rennell. The other two, *fraudulenta* and *brenchleyi* are typical of the Solomons, the former widely spread except on the easternmost islands, and the latter almost confined to them except for an unusual record of five from Bougainville which needs confirmation by other specimens. The distance between the nearest points on Rennell and Guadalcanal, and Rennell and San Cristobal, is about 95 miles. Of the new forms, *kunggana* is a slightly modified *resarta* of the *batesii* complex, so characteristic of Papuasias: *rennellsensis* is a form of the *core* complex not like

	29, <i>rotunda</i>	31, <i>resarta</i>	39, <i>samaraina</i>	73, <i>eurianassa</i>	85, <i>ursula</i>	89, <i>viridia</i>	90, <i>jessica</i>	91, <i>aenea</i>	105, <i>jamesi</i>	110, <i>nivani</i>	114, <i>eurykleia</i>	115, <i>arova</i>	120, <i>eustachius</i>	121, <i>aviena</i>	137, <i>rezia</i>
Samarai			+	+		+			+				+		+
Conflict	+	+													
Nivani		+		+		+		+		+			+		
St. Aignan		+		+	+	+	+						+		
Sudest		+		+			+		+		+		+		
Rossell				+	+		+					+	+	+	

any known, and the only representative of this section in the Louisiade area, although the complex occurs in "Bismarckia" and New Guinea, but not very strongly represented. The new form *rossi*, of the *nemertes* complex is unlike any other. These three, comparatively similar in their markings will be discussed later in the section on Müllerian resemblances.

The *Euploea* of Rennell are of such outstanding interest that large collections from that island, which is almost *terra incognita* so far as insects are concerned (except for those samples collected by the Templeton-Crocker expedition of 1933, the butterflies of which are here described) are greatly needed before its peculiar fauna is ravaged by civilization. I sought information from workers on other groups of insects in the Pacific (Hemiptera, Odonata and Weevils) but little or nothing is known of them on Rennell. Zeuner's study of *Troides* (1943) and Brooks' of *Tenaris* (1950) show that neither of these genera are known on Rennell. I gather from Professor Merrill who was kind enough to answer an enquiry, that the flora is also comparatively unknown. Mayr and Hamlin (1931) have given an account of the birds of Rennell: and on p. 8, Mayr gives the following summary (M.S. amendments in the copy which he kindly sent me make it differ from the published account). "Of these 21 endemic forms 9 (=45 per cent.) point to an origin from the Solomon Islands, 9 (=45 per cent.) point to an origin from Santa Cruz-New Hebrides Islands....In the endemic forms the influence from the Solomon Islands and from the Santa Cruz-New Hebrides Islands is equally strong." The difference between this result and the situation as regards the only known collection of *Euploea* from Rennell is sufficiently striking to emphasize again the need for further knowledge of Rennell *Euploea*. (See addendum (p. 157) for an account of a second collection.)

It appears from maps (Lever, 1936) that Rennell is separated from the Solomons by a channel of great depth. But a long extension towards it from the south-east end of Papua of a tongue of relatively shallow water, at present dotted with islets and shoals, and extending far beyond Rossell, the most easterly of the Louisiades, may have provided stepping stones by which the peculiar forms now only known on Rennell derived their ancestry from Papuan forms, not *via* Bougainville.

(D) *D'Entrecasteaux Archipelago*.

(1) Goodenough: No. 17, *jennessi*, ♂1, ♀1; No. 24, *melia*, ♂7, ♀3; No. 31, *resarta*, ♂6, ♀2; No. 37, *diadema*, ♀2; No. 38, *macgregori*, ♂6; No. 73, *eurianassa*

(in its three named forms), ♂16, ♀13; No. 89, *viridis*, ♂1, ♀6; No. 105, *jamesi*, ♂4, ♀3; No. 111, *callithoe*, ♂2; No. 114, *eurykleia*, ♂7, ♀1; No. 120, *eustachius*, ♂22, ♀17; No. 137, *rezia*, ♂1. Total ♂73, ♀48.

(2) Fergusson: *melia*, ♂10, ♀2; *resarta*, ♂1; *macgregori*, ♂11, ♀2; No. 51, *irene*, ♂3; *eurianassa* (in all forms), ♂10, ♀9; No. 77, a form transitional between *magnipunctata* and 78, *tristis*, ♂1; No. 85, *ursula*, ♀1, and ♀1 trans. to *viridis*; No. 90, *jessica*, ♀1; No. 91, *aenea*, ♂1; *jamesi*, ♂2; *eurykleia*, ♂9, ♀6; No. 115, *arova*, ♂1; *eustachius*, ♂31, ♀3; No. 123, *rhodia*, ♂5, ♀2; *rezia*, ♀2. Total ♂85, ♀29.

(3) Normanby: *macgregori*, ♂1; *eurianassa*, ♂1; *jamesi*, ♂1. Total ♂3.

These three islands have much in common; the only three forms recorded from Normanby occur on both the others. No. 17 *jennessi* (Pl. 4, fig. 5) is peculiar to Goodenough, but a single variant is known from Port Moresby or Yule Island (New Guinea). The *alcatheae* complex is represented by No. 37, *diadema*, on Goodenough, and its close ally, *macgregori*, occurs on all three islands. The rare *irene*, No. 51, on Fergusson is the only member of the *algea* complex in this archipelago. The occurrence of a member of the *sylvester* group, No. 77, on Fergusson is exceptional; no other members have been seen. The *phaenareta* group is well represented by two forms peculiar to this archipelago, *eurykleia* and *arova*, which occur together on Fergusson, and by *callithoe* on Goodenough in the absence of the other two. The *treitschkei* group is represented by four forms in the D'Entrecasteaux Islands.

(E) *Trobriand Archipelago.*

(1) Kiriwina: No. 27, *trobriandensis*, ♂2, ♀1; No. 51, *irene*, ♂8, ♀3; No. 92, *suffusca*, ♂3, ♀1; No. 114, *eurykleia*, ♀1; No. 123, *rhodia*, ♂11, ♀4. Total ♂24, ♀10.

(2) Woodlark: *trobriandensis*, ♂2; No. 28, *nanum*, ♂1; No. 60, *fraudulenta*, ♂15, ♀4; No. 89, *viridis*, ♂11, ♀9; No. 91, *aenea*, ♂3, ♀3; nr. *suffusca*, ♂3; *eurykleia*, ♂6, ♀2; *rhodia*, ♂10, ♀4; No. 124, *messia*, ♀1. Total ♂51, ♀23.

(3) Egum (Yanaba group): *irene*, ♂1; *viridis*, ♂1, ♀5; No. 128, *polymela*, ♀6. Total ♂2, ♀11.

The Trobriand Islands provide two forms in the *batesii* complex (27 and 28) not found elsewhere, although it must be said that *trobriandensis* is not very strongly defined, and only a single *nanum* is known. The rare *irene*, on all three islands, is shared with Fergusson of the previous archipelago. A new form of *treitschkei* (*suffusca*) is peculiar to Kiriwina and Woodlark.

Of considerable interest is the presence of *fraudulenta* and *polymela*, so characteristic of the Solomons; they are the first specimens encountered on passing eastwards from New Guinea. It is noteworthy that *polymela* is the only representative of *nemertes* on Egum, whereas it has not been recorded from the other two islands on both of which another form of *nemertes* (*rhodia*) occurs. The form *messia* is somewhat of a mystery (*vide* taxonomic section).

The Solomons Area.

(A) *The Solomon Islands.*

(1) Nissan or Green Island: No. 47, *illudens*, ♂4, ♀12; No. 88, *eulegnica*, ♂9, ♀9; No. 128, *polymela*, ♂6. Total ♂19, ♀21.

(2) Bougainville: No. 33, *honesta*, ♂7, ♀3; No. 57, *nechos*, ♂8, ♀4; No. 60 *fraudulenta*, ♂18, ♀16; No. 62, *brenchleyi*, ♂5; No. 91, *aenea*, ♂12, ♀10; No. 93, *asyllus*, ♂27, ♀12; No. 102, *pyres* (probably should be No. 103, record only); No. 103, *mangolinella*, ♂6, ♀15; No. 118, *heurippa*, ♂6, ♀7; *polymela*, ♂27, ♀12. Total ♂116, ♀79.

(3) Ovau: *fraudulenta*, ♂3; *polymela*, ♂1. Total ♂4.

(4) Fauro: *fraudulenta*, ♂10, ♀3; *aenea*, ♂5, ♀3; *heurippa*, ♂3, ♀2; *polymela*, ♂1, ♀6. Total ♂19, ♀14.

(5) Faisi: *fraudulenta*, ♂2.

(6) Shortlands, with Alu: *honesta*, ♀4; *nechos*, ♂16; *fraudulenta*, ♂26, ♀6; *aenea*, ♂5, ♀8; *asyllus*, ♂12, ♀4; No. 108, *bismarckiana*, ♂2 (this requires confirmation by further specimens); *heurippa*, ♂12; *polymela*, ♂13, ♀12. Total ♂86, ♀34.

(7) Treasury Island: *nechos* ♂1; *fraudulenta*, ♂3, ♀1; *polymela*, ♂3, ♀1. Total ♂7, ♀2.

(8) Kundikaboko: *fraudulenta*, ♀13; *aenea*, ♀1. Total ♀14.

(9) Choiseul: *honesta*, ♂3, ♀1; *nechos*, ♂3, ♀4; *fraudulenta*, ♂6, ♀1; *aenea*, ♂1; *asyllus*, ♂5, ♀3; *pyres*, ♂2; No. 104, *paucinotata*, ♂1; *heurippa*, ♂5, ♀3. Total ♂26, ♀12.

(10) Bava or Bagga: *polymela*, ♂1.

(11) Vella Lavella: *honesta*, ♂3, ♀3; *nechos*, ♂9; *fraudulenta*, ♂42, ♀9; *aenea*, ♀5; *asyllus*, ♂14, ♀10; *paucinotata*, ♂1; *heurippa*, ♂6, ♀2; *polymela*, ♂10, ♀7. Total ♂85, ♀36.

(12) Ganongga: *fraudulenta*, ♂9, ♀1; *aenea*, ♂1, ♀2; *asyllus*, ♂1, ♀1; *heurippa*, ♂1, ♀1; *polymela*, ♂1, ♀4. Total ♂12, ♀9.

(13) Gizo: *nechos*, ♂1, ♀2; *fraudulenta*, ♂5, ♀2; *asyllus*, ♂3, ♀1; *polymela*, ♂3. Total ♂12, ♀5.

(14) Narovo: *fraudulenta*, ♂1; *asyllus*, ♀1. Total ♂1, ♀1.

(15) Kolombangara: *honesta* ♂3, ♀1; *nechos*, ♀3; *fraudulenta*, ♂50, ♀6; *aenea*, ♂1, ♀1; *asyllus*, ♀1; *paucinotata*, ♂2, ♀1; *polymela*, ♂3, ♀4. Total ♂59, ♀17.

(16) Arundel: *asyllus*, ♂1.

(17) New Georgia: *honesta*, ♂2; *nechos*, ♂1, ♀1; *fraudulenta*, ♂3, ♀2; *asyllus*, ♂4, ♀1; *mangolinella*, ♀1; *polymela*, ♀6. Total ♂10, ♀11.

(18) Rubiana: *honesta*, ♀1; *nechos*, ♂1, ♀1; *fraudulenta*, ♂2, ♀3; *aenea*, ♂1; *asyllus*, ♂1, ♀2; *heurippa*, ♂1, ♀4; *polymela*, ♂4, ♀6. Total ♂10, ♀17.

(19) Rendova: *honesta*, ♂1; *fraudulenta*, ♂15, ♀3; *aenea*, ♂3, ♀3; *asyllus*, ♂2, ♀2; *heurippa*, ♂2, ♀6; *polymela*, ♂3, ♀7. Total ♂26, ♀21.

(20) Ysabel: *honesta*, ♂10, ♀5; *nechos*, ♀3; *fraudulenta*, ♂20, ♀6; *aenea*, ♂5, ♀8; *asyllus*, ♂6, ♀5; *mangolinella*, ♂6, ♀8; *heurippa*, ♂5, ♀8; *polymela*, ♂5, ♀7. Total ♂57, ♀50.

(21) Huleo Islet: *polymela*, ♂10.

(22) Russell Islands (Yandina and Lingatu): *honesta*, ♂1; *fraudulenta*, ♂7; *aenea*, ♂20, ♀32; *asyllus*, ♂1; *polymela*, ♂10, ♀4. Total ♂39, ♀36.

(23) Savo: *fraudulenta*, ♂6, ♀1; *aenea*, ♂1; *pyres*, ♀1; *polymela*, ♂1, ♀2. Total ♂8, ♀4.

(24) Nangatana: *nechos*, ♂3; *fraudulenta*, ♂1; *polymela*, ♂1. Total ♂5.

(25) Florida (with Tulagi): *honesta*, ♂5, ♀1; *nechos*, ♂15, ♀1; *fraudulenta*, ♂54, ♀19, plus one transitional to *pyrgion*; No. 61, *pyrgion*, ♂1, ♀2; *aenea*, ♂23, ♀31; *asyllus*, ♂5, ♀28; *pyres*, ♂56, ♀15; *heurippa*, ♂40, ♀12; *polymela*, ♂31, ♀24. Total ♂230, ♀134.

(26) Guadalcanal (with Aola): *honesta*, ♂24, ♀18; *nechos*, ♂26, ♀2; *fraudulenta*, ♂112, ♀30; *pyrgion*, ♂1; *aenea*, ♂23, ♀31; *asyllus*, ♂5, ♀28; *pyres*, ♂56, ♀15; *heurippa*, ♂40, ♀12; *polymela*, ♂31, ♀24. Total ♂318, ♀160.

(27) Malaita: No. 34, *woodfordi*, ♂4, ♀6; No. 59, *pronax*, ♂11, ♀1; *pyrgion*, ♂29, ♀31; *aenea*, ♂11, ♀10; No. 94, *gerion*, ♂1, ♀1; *heurippa*, ♀1; *polymela*, ♂6, ♀11. Total ♂62, ♀61.

(28) Maramasike: *pyrgion*, ♂5; *aenea*, ♂5. Total ♂10.

(29) Ulawa: No. 58, *prusias*, ♂2; *fraudulenta*, ♂8; *aenea*, ♂3, ♀2; *polymela*, ♂3. Total ♂16, ♀2.

(30) San Cristobal: No. 35, *leucacron*, ♂1; *prusias*, ♂4; *brenchleyi*, ♂38, ♀10; No. 63, *albomarginata*, ♂1, ♀2; No. 89, *viridis* (trans. to *jessica*), ♀1; No. 90, *jessica*, ♂3, ♀3; No. 129, *imitata*, ♂7, ♀3. Total ♂54, ♀19.

(31) Ugi: *prusias*, ♀4; *brenchleyi*, ♂10, ♀2; *jessica*, ♀1; *imitata*, ♀5. Total ♂10, ♀12.

(32) Santa Ana: *prusias*, ♂33; *brenchleyi*, ♂50; *albomarginata*, ♀1; *imitata*, ♂10, ♀2. Total ♂93, ♀3.

(33) Santa Catalina: *prusias*, ♂1.

The accompanying table (p. 134) records the distribution of all forms of *Euploea* known from the Solomons, except for the following islands from which the numbers are too small—Kamaliai, Lofung, Undeka. The fauna has very definite characters: it lacks the complexes of *modesta*, *alcatheae*, *core*, and *algea*, and the whole of the *sylvester* group. The *batesii* section of the *climena* group is represented by three forms peculiar to the Solomons, of which only *honesta* is common.

Forms of *boisduvalii* are numerous but not all widespread. The *treitschkei* group has a form, *aenea*, widely distributed and peculiar to the Solomons with very few exceptions such as Woodlark Island, the nearest to the Solomons of the Papuan area. The form *jessica* only occurs at the eastern end of the group on San Cristobal; a single *viridis* transitional to *jessica* was taken on the same island. The species *asyllus* is not found outside the Solomons and its origin is obscure: it is placed by Corbet in his *eleusina* group of which the only other species is *eleusina* Cramer, 1780, from Java and other Malaysian islands. The two *bismarckiana* are somewhat doubtful, for it is an inhabitant of the Bismarckian area, and not known from Bougainville as might be expected seeing that both specimens are labelled "Shortlands". On the other hand Nissan Island, a link between the Bismarckian and Solomons areas, has two forms belonging to the former and one to the latter. So Bougainville may yet prove to have been a stepping stone. The *phaenareta* group is well represented by *heurippa*, the only form: none of the *callithoe* section have reached the Solomons.

The table shows that there are seven dominating forms—*honesta*, *nechos*, *fraudulenta*, *aenea*, *asyllus*, *heurippa*, *polymela*. It also shows a difference of biological significance at the eastern end of the archipelago; Malaita, Ulawa, Ugi, San Cristobal (*cp.* Lever, 1936) and Santa Ana having peculiarities of their

own (see Plates 7, 8). It is seen that *honestia* is replaced by *woodfordi* and *leucacron*, that *nechos* is replaced by *prusias* and *pronax*, *fraudulenta* by *pyrgion*, *polymela* by *imitata* and *asyllus* by *gerion*. Also, these substitute forms are associated with other, similarly white forms, *brenchleyi* and *albomarginata*, and the strongly white-marked *jessica* replaces the usual *aenea*. These changes will be discussed later. Another case of replacement or substitution is seen in *pyres*. The more heavily spotted *mangolinella* and the less spotted *paucinotata* are mutually exclusive, but the nomino-typical *p. pyres* occurs with *paucinotata* on Choiseul. As pointed out previously, the specimen of *p. pyres* recorded from Bougainville may very well be a poorly spotted *mangolinella*.

Lastly, it would add to the interest of this subject if gaps could be filled, or doubtful records confirmed. From the following island no *Euploea* have been seen—*Buka*, at the north-west end of Bougainville, which might provide interesting links with the Papuasian or Bismarckian areas; *Robroy* and other islets at the eastern end of Choiseul; *Wana Wana*, *Tetipari*, *Vangunu*, *Gatukai* and *Murray I.* on the south and east of New Georgia; *St. George's I.* at the south-east end of Ysabel and sundry islets at the other end; *Gower I.*, north of Cape Astrolabe on Malaita; the "Three Sisters" north of San Cristobal, and the very isolated *Sikai Ana* group, well to the east of Malaita.

(B) *Santa Cruz Islands.*

(1) Matema or Swallow Islands: No. 66, *matemae*, ♀1; No. 75, *moesta*, ♂2; No. 78, *tristis*, ♂1. Total ♂3, ♀1.

(2) Santa Cruz: No. 62, *brenchleyi*, ♀1; No. 64, *era*, ♂19; No. 76, *melander*, ♂4, ♀2; No. 128, *polymela*, ♂1; No. 131, *crucis*, ♂3, ♀1. Total, ♂27, ♀4.

(3) Utupua: No. 60, *fraudulenta*, ♂1; No. 65, *lapeyrousei*, ♀2; *melander*, ♂1, ♀1; No. 91, *aenea*, ♂1. Total ♂3, ♀3.

(4) Vanikoro: No. 1, *brunnescens*, ♂1; *lapeyrousei*, ♂3, ♀22; *melander*, ♂1, ♀1; No. 89, *viridis* trans. to *jessica*, ♀3. Total ♂5, ♀26.

(5) Tikopia or Tucupeia: *brunnescens*, ♂13, ♀1; No. 133, *iphianassa*, ♂5, trans. from *iphianassa* to No. 134, ♂1. Total ♂19, ♀1.

(6) Anuta or Cherry Island: *matemae*, ♂3, ♀2; No. 132, *eustachiella*, ♂1, ♀2. Total ♂4, ♀4.

These 60♂ and 39♀ are interestingly different from the Solomons fauna: two specimens (*brenchleyi* and *polymela*) on Santa Cruz and the *fraudulenta* on Utupua may be examples of wanderers which have their analogues in other areas.

A peculiarity of the Santa Cruz area is the smaller size of the representatives of forms previously noted in the Solomons. Thus, in the *boisduvalii* series, *matemae*, *era*, *lapeyrousei* (Plate 4) are all smaller than the average *fraudulenta* (Pl. 6, figs. 3, 7) from which they have been derived. (It will be seen later that there are three other, small, forms to the south.) Similarly, *crucis* and *eustachiella* are smaller than *polymela*: it is curious that the single *polymela* from Santa Cruz is also small. The five *iphianassa* are noteworthy, for that is the form of the *nemertes* complex found chiefly in the New Hebrides area: it occurs with the characteristically New Hebridean *novarum-ebudum* (No. 134) which raises the problem of their taxonomic status (*vide* what is said about "Species Duplex")

on p. 3). In this area, for the first time, we meet a member of the *lewini* complex (No. 1, *brunnescens* here described as a new form) obviously derived from the New Hebrides, the complex being absent from the Solomons. Further investigation of the Santa Cruz area should be of interest.

The New Hebridesian Area.

(A) *Torres Islands*. No. 60, *fraudulenta*, ♂4, ♀2 (precise locality unknown).

(1) Hiw : No. 78, *tristis*, ♂10, ♀3 ; No. 133, *iphianassa*, ♂8. Total ♂18, ♀3.

(2) Loh : *iphianassa*, ♂1.

(3) Tegua : *fraudulenta*, ♂1 (? a hybrid specimen, abnormal) ; *tristis*, ♂13, ♀5 ; *iphianassa*, ♂2, ♀2. Total, ♂16, ♀7.

(B) *Banks Islands*.

(1) Ureparapara : No. 68, *bakeri*, ♂1 ; No. 77, *magnipunctata*, ♂3. Total ♂4.

(2) Reef Island : No. 64, *era*, ♂7 ; No. 76, *melander*, ♂2, trans. to *tristis*, ♂2 ; No. 134, *novarum-ebudum*, ♂1. Total ♂12.

(3) Valua, or Saddle Island : *bakeri*, ♂1, ♀1 ; *novarum-ebudum*, ♂2. Total ♂3, ♀1.

(4) Pakea : *magnipunctata*, ♂2, ♀4 ; No. 90, *jessica*, ♂3, ♀2 ; *novarum-ebudum*, ♂3. Total ♂8, ♀6.

(5) Vanua Valava : *bakeri*, ♂4, ♀2 ; *novarum-ebudum*, ♀2. Total ♂4, ♀4.

(6) Mota : *bakeri*, ♂1.

(7) Gaua : *bakeri*, ♂10, ♀1 ; *novarum-ebudum*, ♂6, ♀2. Total ♂16, ♀3.

(8) Merelava : *bakeri*, ♂1.

These two groups of islands show the last links with the Santa Cruz group and the commencement of the New Hebridean fauna. No. 60, *fraudulenta* does not extend further south than Tegua, and the single small specimen suggests hybridization between a wandering *fraudulenta* from the north and the smaller forms in the New Hebridesian area, *era* or *bakeri*. The members of the *sylvester* group (*magnipunctata* (Pl. 4, figs. 7, 8) and *tristis* (Pl. 2, fig. 7)) have their headquarters in this area, but *melander* has reached the Santa Cruz area. The *treitschkei* group is represented by *jessica*, and *nemertes* by *novarum-ebudum* whose name speaks for itself.

(C) *New Hebrides*.

(1) Espiritu Santo : No. 2, *lilybaea*, ♂7, ♀2 ; No. 68, *bakeri*, ♂31, ♀15 ; No. 90, *jessica*, ♂2, ♀2 ; No. 133, *iphianassa*, ♂1 ; No. 134, *novarum-ebudum*, ♂12, ♀11. Total ♂53, ♀30.

(2) Dolphin Island : *lilybaea*, ♂1.

(3) Aore : *novarum-ebudum*, ♀1.

(4) Malo : *lilybaea*, ♀1 ; *bakeri*, ♂4 ; No. 78, *tristis*, ♂1, ♀1 ; *novarum-ebudum*, ♂2. Total ♂7, ♀2.

(5) Aoba : *tristis*, ♂2, ♀3, trans. to *magnipunctata* (No. 77), ♂1, ♀1 ; *novarum-ebudum*, ♂2, ♀3. Total ♂5, ♀7.

(6) Pentecost : *lilybaea*, ♂3 ; *bakeri*, ♂8 ; *novarum-ebudum*, ♂7, ♀7. Total ♂18, ♀7.

(7) Ambrim : *novarum-ebudum*, ♀1.

(8) Malekula or Mallicolo : *lilybaea*, ♂1, ♀3 ; *bakeri*, ♂19, ♀5 ; *tristis*, ♂8, ♀3 ; *jessica*, ♂3, ♀4 ; *novarum-ebudum*, ♂3, ♀4 ; *iphianassa*, ♀1. Total ♂34, ♀20.

(9) Epi : *lilybaea*, ♂4, ♀1 ; *bakeri*, ♂18, ♀5 ; *tristis*, ♂4 ; *novarum-ebudum*, ♂38, ♀7. Total ♂64, ♀13.

(10) Tongoa : *bakeri*, ♂1.

(11) Mai : *jessica*, ♂1, ♀1.

(12) Efate, Vate, or Sandwich Island : *lilybaea*, ♂1, ♀2 ; *bakeri*, ♂2, ♀1 ; *tristis*, ♂1 ; *jessica*, ♂4, ♀2 ; *novarum-ebudum*, ♂2, ♀4. Total ♂10, ♀9.

(13) Erromanga : *lilybaea*, ♀2.

(14) Tana : *lilybaea*, ♂3, ♀2 ; No. 67, *torvina*, ♂11, ♀1 ; No. 96, *tulliolus* with No. 98A, *forsteri*, ♂4, ♀3 ; *novarum-ebudum*, ♀1 ; *iphianassa*, ♂18, ♀2. Total, ♂36, ♀9.

(15) Aneityum : *lilybaea*, ♂1 ; *torvina*, ♂1, ♀2 ; *tristis*, ♂1 ; *iphianassa*, ♂2, ♀2. Total ♂5, ♀4.

The *Euploea* fauna of New Hebrides is represented by only eight forms : the area is linked with Santa Cruz by the *lewinii* complex which, curiously, seems absent from the Torres and Banks groups : the one race *lilybaea* is peculiar to New Hebrides. Of the two small forms of *boisduvalii*, *bakeri* is widespread, *torvina* only on the most southern isles. The *sylvester* group is represented by *tristis*, which may have originated here. *Treitschkei* is represented by one of its most strikingly marked forms, *jessica*, but is not recorded from the southern isles. The *nemertes* complex has two forms, one characteristic of New Hebrides and thus named, and the other *iphianassa* also found in New Caledonia. The form *novarum-ebudum* easily grades into *macleayi* of Fiji. The southern isles, Tana and Aneityum, differ from the northern by the presence of the species *tulliolus*, which occurs in the typical form *tulliolus* characteristic of Australia and *forsteri*, proper to Fiji, and by the lack of *bakeri* and, possibly, *treitschkei*. The New Hebrides area proper differs from the Banks and Torres groups in some respects but the whole group is linked with Santa Cruz to the north and New Caledonia to the south.

New Caledonia.

(A) *New Caledonia.* No. 3, *montrouzieri*, ♂61, ♀42 ; No. 54, *helcita*, ♂4 ; No. 69, *rileyi*, ♂4, ♀3 ; No. 78, *tristis*, ♂2, ♀1 ; No. 90, *jessica*, ♂1, ♀1 ; No. 96, *tulliolus*, ♂1, ♀1 ; No. 98A, *forsteri*, ♂5, ♀5 ; No. 99, *adyte*, ♂2, ♀3 ; No. 133, *iphianassa*, ♂1. Total ♂81, ♀56.

Île des Pins. Viette (1950) records *montrouzieri* from the Île des Pins, under its old name *helcita* Boisduval, and "*schmeltzi whitmei*", now known to be the *helcita* of Boisduval, from the same locality. Only nine forms are known from New Caledonia, of which *helcita* is confined to it (with the Loyalty Isles). This species is interesting because with the exception of it and *schmeltzi* (No. 56) in Samoa, the *algea* complex does not extend east of the Trobriand Archipelago though occurring in Guam and Palau, and in Australia. The representative of the *lewinii* complex, *montrouzieri*, is peculiar to New Caledonia : *boisduvalii* *rileyi* is shared with Lifu, like *tulliolus adyte* : both of these are confined to the New Caledonian area. The almost complete absence of the *nemertes* complex is surprising : the single *iphianassa* may have been a wanderer. The area is

linked with New Hebrides by *tristis* and *jessica*, and, as in New Hebrides, it seems that *tulliulus* having established itself in the variable form *forsteri*, has been invaded by the nomino-typical *tulliulus* from Australia, and these have inter-bred with the result seen in an interesting collection which Professor Charles L. Remington of Yale University made on New Caledonia and kindly sent to me to be identified. It consists of *t. tulliolus* ♂1, ♀1, *forsteri*, ♂5, ♀5, *adyte*, ♀2, and ranges from the maximal spotting, through the less strongly marked *forsteri* to the brown and poorly spotted *adyte*. The two *tulliulus* forms lack a little of the purple sheen of Australian specimens but both have the characteristic spot D.10 on both surfaces of the fore wing; the male also has D.2 below. These spots are lacking in the *forsteri* and *adyte* specimens.

The comparatively small number of endemics in New Caledonia, of which *helcita* is the only really isolated example, is surprising since the island is largely of sedimentary formation and believed to be a very ancient land area. (See Jeannel, 1942, p. 232 *et seq.*). Good (1947) writes of the botany, that New Caledonia is of greatest interest for its marked endemism, with over 100 endemic genera of plants ranging over 27 families. Some useful references to the island are given by Alexander (1948). Cheesman (1952) in the abstract of a communication, says New Caledonia "is considered to have formed part of the Australian shelf until the mid-Tertiary, connected with New Guinea by a chain of islands which were raised by the tectonic movements of the late Miocene. . . . The extremely limited fauna and flora are Australasian with Papuan influence". The *Euploea* fauna, with the exception of *helcita*, is characteristic of the southern Pacific.

(B) *Loyalty Islands*. No. 54, *helcita*, ♂2.

(1) Uvea : *helcita*, ♂1 ; No. 69, *rileyi*, ♂1 ; No. 99, *adyte*, ♂1. Total ♂3.

(2) Lifu : *helcita*, ♂28, ♀13 ; *rileyi*, ♂30, ♀9 ; *adyte*, ♂17, ♀11. Total ♂75, ♀33.

(3) Maré : No. 55, *aglaina*, ♂1, ♀2 ; *adyte*, ♂1 ; *tulliulus*, form very near *incompta*, ♂1. Total ♂3, ♀2.

There is close relationship with New Caledonia. No. 54, *helcita* (formerly known as *whitmei*) is a well marked species : the subspecies *aglaina* is peculiar to the Loyalties, like *rileyi* which is very easy to distinguish by its spotting from its near allies, the small forms of *boisduvalii*, to the north.

Australian.

The genus *Euploea* in Australia extends from islands in Torres Straits via Cape York through Queensland as far as New South Wales and South Australia, whence a few specimens of No. 43, *corinna*, have been seen. Many *corinna* have been examined with the only data "Eureka, Northern Territory, S. Australia". This place cannot be traced, it may have been an ephemeral camp. To the north-west *Euploea* occurs on the coast of Admiralty gulf, and the neighbourhoods of Darwin, Daly river and Roper river have provided a number of specimens. From Western Australia I have seen specimens from Brock's Creek, Derby and Dawson districts, and Geraldton.

The following islands have provided a few specimens which I have seen, or records by Waterhouse & Lyell (1914), or Waterhouse (1932), and Musgrave (1948):—

Torres Straits, Banks Island: No. 74, *inconspicua* (syn. *crithon*); No. 80, *sylvester* (records). Darnley Island: No. 30, *belia*; No. 49, *amycus*; *sylvester*; No. 96, *tulliolus*; No. 101, *niveata*. All recorded. Murray Island: *belia* (recorded). Thursday Island: No. 43, *corinna*; *amycus* (recorded); No. 50, *reginae* (Pl. 9, fig. 5); *tulliolus*; *niveata* (recorded). Prince of Wales Island: *sylvester* (recorded). Horn Island: *sylvester* (recorded).

Cape York is here mentioned for interest: *corinna*, *amycus*, *inconspicua*, *sylvester* with *dardanoides* and *pelor*, *niveata*. Lizard Island: *corinna*.

Queensland, Frankland Island: *tulliolus*. Ross Island: *tulliolus*. Magnetic Island: *tulliolus*.

The following is a list of forms known from Australia:—

No. 12, *macleari*; No. 30, *belia*; No. 41, *eichhorni*; No. 49, *amycus*; No. 50, *reginae*; No. 74, *inconspicua* (= *crithon*); No. 79, *pelor*; No. 80, *sylvester*; No. 81, *dardanoides*; No. 96, *tulliolus*; No. 98A, *forsteri* (from Port Denison in company with *tulliolus*); No. 100, *darchia*; No. 101, *niveata*; No. 132, *eustachius* (a single ♂ from "Queensland"); and No. 136, *usipetes* (from Cape York and Thursday Island (recorded as "*hippias*" by Miskin). Some features of the Australian *Euploea* fauna are noteworthy. The *lewinii* complex is entirely lacking: *climena* is represented by *macleari* elsewhere only known from Christmas Isle in the Indian Ocean; the *batesii* complex only occurs as *belia* in the Torres Straits, like *monilifera* of the *alcathoe* complex which is otherwise well represented by *eichhorni*, peculiar to Australia. The *core* complex likewise has an Australian representative *corinna* with a relationship to be discussed later. The *algea* complex has a little known form *reginae* here described for the first time, in the north-west: the *boisduvalii* complex is lacking. The *sylvester* group is well represented by the nomino-typical form confined to Australia; *inconspicua* has only been found in the Torres Straits. The *treitschkei* group is entirely absent, the *tulliolus* group well represented by the nomino-typical form, and two others confined to Australia. No representatives of the *phaenareta* group occur in Australia, and the almost universally distributed *leucostictos* group is with one exception only known by a single *eustachius* possibly doubtfully labelled "Queensland". The exception is *usipetes* from the Torres Straits.

Fijian.

(A) Fiji.

(1) Yasawa group: No. 4, *eschschoitzii*, ♂4. Waisala: No. 70, *herrichii*, ♂2; No. 98A, *forsteri*, ♂1, ♀1. Naviti: *herrichii*, ♀1; *forsteri*, ♀2. Total ♂7, ♀4.

(2) Viti Levu: *eschschoitzii*, ♂48, ♀17; *herrichii*, ♂80, ♀42; *forsteri* (including Viwa or Rewa Islet, ♂1, ♀3), ♂31, ♀13; No. 135, *macleayi*, ♂6, ♀3. Total ♂166, ♀78.

(3) Bega or Mbengha: *macleayi*, ♂3, ♀2.

(4) Moturiki: *eschschoitzii*, ♀1; *herrichii*, ♀1; *forsteri*, ♀1. Total ♀3.

(5) Ovalau: *eschschoitzii*, ♂23, ♀8; *herrichii*, ♂26, ♀13; *forsteri*, ♂6, ♀2; No. 98B, *incompta*, ♂1; *macleayi*, ♂12, ♀14. Total ♂68, ♀37.

- (6) Mokogai : *herrichii*, ♂1.
- (7) Vanua Levu : *eschsoltzii*, ♂14, ♀7 ; *herrichii*, ♂8, ♀7 ; *forsteri*, ♂18, ♀6 ; *incompta*, ♂4, ♀1 ; *macleayi*, ♀1. Total ♂44, ♀22.
- (8) Taveuni : *eschsoltzii*, ♂6, ♀1 ; *herrichii*, ♂10, ♀3 ; *forsteri*, ♂3, ♀2 ; *incompta*, ♂1 ; *macleayi*, ♂1, ♀1. Total ♂21, ♀7.
- (9) Koro : *eschsoltzii*, ♂1 ; *herrichii*, ♂5, and trans. to *mangoensis*, ♂16 ; No. 71, *boisduvalii*, ♂2 ; No. 72, *mangoensis*, ♂4, ♀1 ; *incompta*, ♂3 ; No. 134, *novarum-ebudum*, ♂1 ; *macleayi*, ♂4, ♀1. Total ♂36, ♀2.
- (10) Ngau : *eschsoltzii*, ♂3 (including trans. to No. 9, *walkeri*) ; *herrichii*, ♂1. Total ♂4.
- (11) Ono : *eschsoltzii*, ♀1 (a brownish aberration rather suggesting No. 2, *lilybaea*) ; *walkeri*, ♂1 ; *herrichii*, trans. to *mangoensis*, ♂4 ; *macleayi*, ♂6. Total ♂11, ♀1.
- (12) Kandavu : *eschsoltzii*, ♂1, ♀3 ; *herrichii*, ♂1 ; do : trans. to *mangoensis*, ♂4 ; *forsteri*, ♀2 ; *incompta*, ♂1 ; *macleayi*, ♂4, ♀7. Total ♂11, ♀12.
- (13) Matuku : *walkeri*, ♂1 ; *incompta*, ♂1. Total ♂2.
- (14) Totoya : *forsteri*, ♀1 ; *incompta*, ♂1 ; *macleayi*, ♂1, ♀2. Total ♂2, ♀3.
- (15) Moala : *mangoensis*, ♂4 ; *forsteri*, ♂4, ♀1 ; *incompta*, ♂3 ; *macleayi*, ♂2, ♀2. Total ♂13, ♀3.
- (16) Vanua Vatu : *walkeri*, ♂2.
- (17) Kambara : *walkeri*, ♂4.
- (18) Fulanga : *walkeri*, ♂1.
- (19) Lakemba : *walkeri*, ♂5, ♀6 ; *herrichii*, ♂1 ; *forsteri*, ♂13, ♀2 ; *incompta*, ♂1 ; *macleayi*, ♂3, ♀3. Total ♂23, ♀11.
- (20) Naiau : *walkeri*, ♂2 ; *incompta*, ♂1. Total ♂3.
- (21) Thithia : No. 5, *lauensis*, ♂1 ; *walkeri*, ♂4, ♀2 ; *herrichii*, ♂1, trans. to *mangoensis*, ♂1 ; *mangoensis*, ♂4, ♀3 ; *incompta*, ♂7, ♀2 ; *macleayi*, ♀5. Total ♂18, ♀12.
- (22) Mango : *lauensis*, ♂5 ; *walkeri*, ♀2 ; *mangoensis*, ♂3, ♀1 ; *incompta*, ♂8, ♀4 ; *macleayi*, ♂3, ♀1. Total ♂19, ♀8.
- (23) Munia : *eschsoltzii*, ♂5, ♀5 (including trans. to *lauensis* and *walkeri*) ; *lauensis*, ♂6, ♀3 ; *walkeri*, ♂1 ; *mangoensis*, ♂3 ; *incompta*, ♂10, ♀1. Total ♂25, ♀9.
- (24) Vanua Mbalavu : *eschsoltzii*, trans. to *lauensis*, ♂13, ♀4, trans. to *walkeri*, ♂5 ; *lauensis*, ♂28, ♀3 ; *walkeri*, ♂1, ♀1 ; *mangoensis*, ♂17, ♀3 ; *incompta*, ♂31, ♀4 ; *macleayi*, ♂4, ♀13. Total ♂99, ♀28.
- (25) Naitamba : *lauensis*, ♂1, trans. to *walkeri*, ♀1 ; *incompta*, ♂1 ; *macleayi*, ♂1. Total ♂3, ♀1.
- (26) Fotuna : *walkeri*, ♂4, ♀1.
- (27) Wallis Island : No. 6, *distincta*, ♂2 ; *mangoensis*, ♂3, ♀5. Total ♂5, ♀5.
- (28) Ellice group (see Hopkins, 1927, p. 14) : *distincta*, ♂16, ♀10 ; *walkeri*, ♀1 ; *herrichii*, ♀1. Total ♂16, ♀2.
- (29) Union Island or Tokelau : *walkeri*, ♂1.

The Fijian area as a whole is especially characterized by the *lewinii* complex which must have developed there : it extends as far north only to Santa Cruz as *brunnescens* (No. 1), but is the easternmost representative of *Euploea* by the subspecies *walkeri*, the only one in Tahiti. The *boisduvalii* and *nemertes* forms

[illegible]

are obviously of north-western origin : the former has, apparently by long isolation, produced the peculiar form *herrichii*, but *mangoensis* is very similar to *fraudulenta* of the Solomons. The *nemertes* complex is represented abundantly by the autochthonous *macleayi*, but the capture on Koro of a *novarum-ebudum* is interesting, it was possibly a wanderer. The *syvester* and *treitschkei* groups are entirely absent, and also the more northern *phaenareta* group.

The Fijian *Euploea* were so thoroughly discussed by Poulton (1924) that it is only necessary here to refer to his study. But a tabular statement (p. 141) embodying later accessions to collections, supports his conclusions as to the forms of *lewinii*, *boisduvalii* and *tulliulus*. His map should be consulted (*loc. cit.* p. 682). Finally, it is interesting to note that the form of the *lewinii* complex which is most widely distributed, possibly because it is a wanderer, is *walkeri*, the one chiefly found in the more isolated islands in the south of the Fiji group, as well as being the one which has spread furthest to the east in the Pacific (*vide infra*, p. 152, note 3 on Mayr's remarks). There are islands from which no *Euploea* are known, and those in the far south of the Lau group would be especially interesting, *e.g.*, from south to north, Tuvana i tholo and Tuvanaira, Ono i lau, Vuata Vatoa and Vatoa, Fulanga (a single *walkeri* is known), Ongealevu, a whole group between the last named and Lakemba, four small islands east of Naiaua and Thithia and three west of Vanua Mbalavu. Other islands in the western section of Fiji, still unknown, lie to the east of Taveuni and Vanua Levu, of which the isolated Ngelelevu might prove to be especially interesting. Further knowledge of the proportions between forms in the Yasawa group is required, and Vatulele to the south of Viti Levu is quite unknown.

(B) *Tonga or Friendly Islands*. No. 7, *lewinii*. Tonga ♂25, ♀3; Haapi, ♂7, ♀6; Vavau, ♂35, ♀5; Tongatabu, ♂126, ♀8. Total ♂193, ♀22. The fact that all the 215 *Euploea* taken in this group belong to the one subspecies gives good grounds for belief that it is the only representative. It will be interesting to see if, in future years, the wandering *walkeri* may establish itself.

(C) *Niue or Savage Island*. No. 10, *perryi* is the only race recorded, in various forms. Total, ♂18, ♀3.

(D) *Samoa or Navigator's Islands*. "Samoa": No. 8, *bourkei*, ♂16, ♀5; No. 10, *perryi* (form "*intermedia*" Moore), ♂1 (this is the specimen to which Poulton referred (*loc. cit.*, p. 586), as a form of *walkeri* with H.W. pattern of *eschscholtzii*); No. 56, *schmeltzi*, ♂23, ♀14. Total ♂40, ♀19.

(1) Savai : *schmeltzi*, ♂24, ♀3.

(2) Upolu : *schmeltzi*, ♂80, ♀33.

(3) Tutuila : *bourkei*, ♂1.

(4) Monono : *schmeltzi*, ♂1.

The distribution of *schmeltzi* and its apparent absence from Tutuila was discussed by Hopkins (1927). He refers to an observation by Buxton in the district of Aleipata, on Upolu. "... At about 9 a.m. he found the butterflies in numbers flying out from the mainland towards the small outlying islands of Namua and Nuutele . . . a distance of more than a mile in the case of Nuutele." The presence of this member of the *algea* complex in Samoa, and of other members (*helcita* and *aglaina*) in the New Caledonian area, is a good example of discontinuity,

for the other members of the complex in the Pacific are far away, in Australia or in Guam and Palau in the North Pacific.

(E) *Union Island or Tokelau*. A ♂ *walkeri* in the British Museum (Nat. Hist.) labelled "Atafu, Union Point, J. J. Lister" and referred to by Hopkins (1927, p. 15) as from "Atafu, Union Island".

(F) *Cook, or Savage Islands*. (1) Aitutaki: No. 10, *perryi* ("unicolor"), ♂5, ♀1.

(2) Rarotonga: *perryi* ("indistincta"), ♂2, ♀2. Total ♂7, ♀3.

(G) *Tahiti or Society Islands*. No. 9, *walkeri*. "Tahiti", ♂50, ♀22; Eimeo, ♂8, ♀6; Moorea, ♂4, ♀1. Total ♂62, ♀29. This is the easternmost habitat of *Euploea*. It is curious that the very dark *perryi* should come between the two most strongly white spotted races, *bourkei* and *walkeri* (Pl. 2, fig. 4).

North Pacific (Micronesia).

I have not considered any islands save those which might seem to be a link with all that has previously been considered. Thus, the Philippines, Formosa, and the Riu Kiu Islands have not been included. But *Euploea* is found in Palau and Guam: Yap, in between, has furnished no specimens that I know of.

(A) *Palau or Pelew*. The very curious No. 53, *abjecta*, of the *algea* complex, is the only *Euploea* in this area, but is also found on the Philippines. I have examined ♂22, ♀7 from Palau and ♂5 from the Philippines. This distribution is curious, for, by the atlas, the faunal relations of Palau might be expected to be with Gilolo (Halmahera) of the northern Moluccas, between which and Palau there are reefs, and shallower water than between Palau and the Philippines. The explanation is possibly to be sought in sea-traffic from the Philippines, but it must have been long ago for *abjecta* is a very peculiar species.

(B) *The Marianne Islands*. The relations with the Philippines are again exemplified in Guam by No. 119, *leucostictos kadu*, closely related to *oculata* Moore, 1883, from Mindanao, with subspecies *okinawensis* Sonan, 1926, from Formosa, *phane* Doherty, 1891, from Engano, *hobsoni* Butler, 1877 (syn. *hewitsonia* Bryk, 1937), from Formosa, and *coelestis*, Fruhstorfer, 1901, from Tonkin. The species complex *leucostictos* is said by Fruhstorfer (1910) to be "essentially a Macro-Malaysian species, dominant everywhere on the large Sunda Islands and their satellites". I have examined the following specimens of *kadu*.

Guam, ♂97, ♀29; Saipan, ♂10, ♀7. Total ♂107, ♀36.

It is interesting, having considered *abjecta*, to find in the Mariannes another representative of *algea*, No. 52, *eleutho* (formerly confused with the so-called *helcita* now known as *lewinii*). It seems as isolated as *abjecta*. I have examined ♂100, ♀7 from Guam and ♂10, ♀4 from Saipan. For an account of the insects of Guam see Swezey (1942).

According to Teiso Esaki (1950) the insects of the Marianne Islands are "more closely related to the Oriental Region than any other groups in the Pacific". Endemic species and genera are few in number. The Palau or Pelew Islands, including Yap, have much the richest fauna among Micronesian Islands, and contain a number of interesting endemic genera and species. The following occur in Palau but not elsewhere in Micronesia: Mutillidae, Scolidae, Crabronidae, Tipulinae, Rutelidae, Dynastidae, Passalidae, Papilionidae, and many genera.

It is concluded that the Palau Islands, much richer than other Micronesian and Polynesian Islands, should belong to the *Melanesian* region. The writer places in Micronesia the Caroline high islands (Kusaie, Ponape, Truk), the Marianne and Bouin Islands. Dr. Robert W. L. Potts kindly told me that on his visit to Truk in 1949 he took no *Euploea* in three months.

PART 5. RELATIONSHIPS OF EACH SUB-AREA.

The distribution of the *Euploea* here considered confirms the view that the islands of Melanesia, etc., derived their fauna from the west. It is only necessary to trace the genus to its extreme south-eastern point to see how the number of forms diminishes until, in Tahiti, only one remains. There seem to be three lines along which distribution has taken place, north-eastern, south-eastern and southern.

1. The north-eastern route.

Few *Euploea* have followed this: it concerns only the Palau and Marianne Islands, and does not reach the Sandwich Isles. The forms found there are two members of the *algea* complex (Nos. 52 and 53) and one *leucostictos* (No. 119).

2. The main trend from Malaysia and New Guinea to the south-east.

But it seems doubtful if the route to the Solomons lay through the Bismarck Archipelago, for comparison of the two faunas shows great differences. A recent study of the Amathusiid genus *Tenaris* by Brooks (1950) does however suggest links between these two areas. Thus *T. phorcas* Westwood, 1858, is generally distributed over the Solomon Islands and Bismarck Archipelago, and several forms are mentioned as occurring on some Islands in each area. But it may be noticed in this connection that the Admiralty Isles have a form of *phorcas* entirely confined to those islands, just as in the case of *Euploea*.

An attempt has been made in the following table to show the relations of the *Euploea* of the Papuan area with those of the Bismarckian and Solomons areas; closely allied forms in different columns are indicated by asterisks. (There are, of course, *Euploea* in New Guinea which are not included in this study as they have not dispersed from New Guinea into the islands here considered.) If a form in Papuasias occurs in the Louisiade, D'Entrecasteaux, or Trobriand Archipelagoes the corresponding initial letter, L, D, or T, is appended in brackets. Quite a number of forms are thus marked, but they have gone no further except for No. 31, which has reached Rennell in the Solomons. Nos. 27 and 29 are close to No. 26 of the Bismarckian area, and No. 33 may have come from the same stock, but has become much more distinct. No. 116 of Bismarckia is near to No. 118 of the Solomons: they seem closely related to *phaenareta* from the Moluccas. The record of No. 128 under Papuasias depends upon a single specimen from an island in the Trobriand Archipelago.

No.	PAPUASIAN	BISMARCKIAN	SOLOMONS
11		<i>doretta</i>	
13		<i>nobilis</i>	
14	<i>lugens</i>		
15	<i>misagenes</i>		
16	<i>weneri</i>		
17	<i>jennessi</i>		

No.	PAPUASIAN	BISMARCKIAN	SOLOMONS
18		<i>insulicola</i>	
19	<i>cerberus</i> *	<i>cerberus</i>	
20		* <i>subpunctata</i>	
21		* <i>griseitincta</i>	
22		* <i>obscura</i>	
23		<i>eboraci</i>	
24	<i>melia</i> (D)		
25	<i>catana</i>		
26		* <i>auritincta</i>	
27	<i>trobriandensis</i> (T)*		
28	<i>nanum</i> (T)		
29	<i>rotunda</i> (L)*		
31	<i>resarta</i> (L, D)*		
32			* <i>kunggana</i> (Rennell only)
33			<i>honesta</i>
34			<i>woodfordi</i>
35			<i>leucacron</i>
36	<i>coffea</i>		
37	<i>diadema</i> (D)		
38	<i>macgregori</i> (D)		
39	<i>samaraina</i> (L)		
42		<i>lacon</i>	
44			<i>rennellensis</i> (Rennell only)
45		<i>umboina</i>	
46		<i>subnobilis</i>	
47		<i>illudens</i>	
48		<i>mathiasana</i>	
51	<i>irene</i> (D, T)		
57			<i>nechos</i>
58			<i>prusias</i>
59			<i>pronax</i>
60-66			<i>boisduvalii</i> forms
73	<i>eurianassa</i> (L, D)		
74	<i>inconspicua</i>		
75	<i>moesta</i>		<i>moesta</i>
76	<i>melander</i>		<i>melander</i>
78			<i>tristis</i>
82		<i>treitschkei</i>	
83	<i>eugenia</i>		
84	<i>dampierensis</i>		
85	<i>ursula</i> (L, D)	<i>ursula</i>	
86	<i>gaedei</i>	<i>gaedei</i>	
87		<i>caerulescens</i>	
88		<i>eulegnica</i>	
89	<i>viridis</i>	<i>viridis</i>	(transitional)
90		<i>jessica</i>	<i>jessica</i>
91	<i>aenea</i> (D, T)		<i>aenea</i>
92	<i>suffusca</i> (T)		
93			<i>asyllus</i>
94			<i>gerion</i>
95	<i>dudgeonis</i>		
97	<i>goodenoughi</i> (D)		

No.	PAPUASIAN	BISMARCKIAN	SOLOMONS
102			<i>pyres</i>
103			<i>mangolinella</i>
104			<i>paucinotata</i>
105	<i>jamesi</i> (D)*		
106	<i>phokion</i>		
107	<i>salpinxoides</i>		
108		<i>*bismarckiana</i>	
109		<i>*manusi</i>	
110	<i>nivani</i> (L)		
111	<i>callithoe</i> (D)		
112	<i>hansemanni</i>		
113		<i>admiralia</i>	
114	<i>eurykleia</i>		
115	<i>arova</i>		
116		<i>unibrunnea*</i>	
117		<i>browni</i>	
118			<i>*heurippa</i>
120	<i>eustachius</i> (L, D)		
121	<i>aviena</i> (L)		
122	<i>erima</i>		
123	<i>rhodia</i>		
125		<i>affinita</i>	
126		<i>perdita</i>	
127		<i>pulchella</i>	
128	<i>polymela</i> (T)		<i>polymela</i>
129			<i>imitata</i>
130			<i>rossi</i> (Rennell only)
131			<i>crucis</i>
132			<i>eustachiella</i>
133			<i>iphianassa</i>
137	<i>rezia</i> (L, D)		

The scanty examples of near relationship between Papuasias and the Solomons make it seem unlikely that there has been direct transit from New Guinea via the three archipelagoes (L, D, T). So many of the Papuasian forms have no representatives in the Solomons; the direct route through the Louisiades has resulted only in two novelties herein described, Nos. 32 and 44.

Certain *Euploea* in the Solomons are so well defined that they seem to have developed there; such are No. 33, *honesta* (Pl. 6, figs. 1, 5), with its derivatives *woodfordi* (Pl. 7, figs. 1, 5) and *leucacron* (Pl. 8, fig. 1), No. 57, *nechos* (Pl. 6, figs. 2, 3), with its derivatives *prusias* (Pl. 8, figs. 2, 6), and *pronax* (Pl. 7, figs. 2, 6), No. 93, *asyllus* (Pl. 6, figs. 4-8) with *gerion* (Pl. 7, figs. 4, 8), and No. 102, *pyres*.

The groups distinguished by Corbet within the genus *Euploea* (pp. 4-8) will be considered as regards their representation in the Solomons.

A. The *climena* group.

Completely unrepresented are the complexes of *lewinii*, *climena*, *modesta*, *wallacei* and *alcathoe*. The *batesii* complex, so well represented in Papuasias, with one form in Bismarckia, has the newly described subspecies No. 32, *kunggana*,

on Rennell Island, geographically part of the Solomons group but faunistically here included in Papuasia.

B. The *core* group.

The *core* complex has No. 44, *rennellensis*, to which the remarks about *kunggana* also apply; *boisduvalii* is represented strongly by Nos. 60–66.

C. The *sylvester* group.

This is unrepresented in Bismarckia, and the very scanty representation in the Solomons seems to have come from Papuasia (Nos. 75, 76).

D. The *treitschkei* group.

The puzzling *treitschkei* group has one predominant form *aenea* (No. 91) which seems to have developed in the Solomons and feebly introduced itself into Papuasia. The strongly-marked forms of *jessica* (No. 90) which occur in Bismarckia and New Hebrides are found in the Solomons only on San Cristobal and Ugi, which is an exceptional distribution for *Euploea*.

E. The *eleusina* group.

The small *eleusina* group is only known in the general area under discussion by No. 93, *asyllus* and its derivative *gerion*. The only other species complex is *eleusina* from Java, Sumbawa, Celebes, etc.

F. The *tulliulus* group.

Except for *pyres* which has been already mentioned, this very large group is unrepresented in the Solomons, but abundant in Papuasia and feebly represented in Bismarckia.

G. The *phaenareta* group.

This is considered here in two sections, *callithoe*, and *phaenareta* proper. The former abounds in Papuasia, also occurring in Bismarckia, but has not reached the Solomons. The latter, absent from Papuasia but represented by one form (No. 116, *unibrunnea*) in Bismarckia, is abundantly represented throughout the Solomons by *heurippa*, No. 118, which is near to *unibrunnea*.

H. The *leucostictos* group.

The *nemertes* complex is widely distributed throughout the general area discussed in this paper (with the exception of Australia), but the form which is characteristic of the Solomons, No. 128, *polymela*, has less affinity with Papuan or Bismarckian forms than with a form in the Moluccas. This will be discussed later.

3. The southern line of distribution.

The route from New Guinea to the northern coast of Australia seems to have been taken by *Ornithoptera* and *Tenaris*, and examples may be found in *Euploea*. It is noteworthy that no member of the eminently South Pacific and abundant *lewinii* complex, and no member of the whole, widespread, groups of *treitschkei*, *phaenareta* or *leucostictos* are known from Australia except for No. 136, *usipetes* (*vide infra*).

The forms *belia* of *batesii*, and *monilifera* of *alcathoe* (Nos. 30 and 40) are apparently derived from New Guinea. The *sylvester* group has derived No. 74, *inconspicua*

from the north, but *sylvester* itself is so characteristically Australian that it must have developed there. The interesting *magnipunctata*, No. 77 (Pl. 4, figs. 7, 8), is nearest to the New Hebridean and New Caledonian *tristis*, but it may have developed from a *sylvester* with reduced spots. The form *tristis*, No. 78, is unknown in Australia.

The *tulliolus* complex has an enormous distribution in Asia, but is unknown in Bismarckia and the Solomons; another complex in the group, *pyres*, is unknown outside the Solomons area, and the third complex, *stephensii*, strongly represented in Papuasias area but weakly in Bismarckia, is absent from Australia.

Besides these three obvious lines of distribution there are links between Australia and the Moluccas, and other islands in the Malaysian Archipelago. The *climena* group has a well marked species on Christmas Island, south of Java; this is No. 12, *macleari* and the Australian "*malindeva*" is the same. It may be said that other forms of *climena* are found in Buru.

The *core* group provides the typically Australian *corinna*, No. 43. But there seems nothing to distinguish this from *coerti* Kalis, 1933, of Bali, very little known and apparently rare. One can only conjecture whether *coerti* found northern Australia less crowded than Bali and having arrived there thrived in the empty spaces. In the section on taxonomy and distribution the presence of *corinna* on Kisser Island was noted. A form described for the first time here is No. 50, *reginae* in the *algea* complex (Pl. 9, fig. 5). It occurs on the north-west coast of Australia and seems very near to *eleutheria* Fruhstorfer, 1910, of Teon, *sacerdos* Butler, 1882, of Tenimber and Timor Laut (Pl. 9, fig. 1), and *ancile* Fruhstorfer, 1910, of Dammer and Babber. The *tulliolus* group provides, in the *darchia* complex, the form *niveata*, No. 101 (Pl. 9, fig. 7) which seems close to *arisbe* C. & R. Felder, 1865, of Timor (Pl. 9, fig. 3) (see Corbet, 1943, p. 146 and Zeuner, 1943, p. 161). Lieftinck (1949a) writes in a footnote to p. 236 "Tillyard thinks that the rich Australian Gomphid fauna must have entered this continent long ago via Timor, since true Gomphinae do not occur in Papua". Lastly, in the *leucostictos* group, No. 136, *usipetes* provides two specimens from Cape York and Thursday Island. Its headquarters, in this form, are the Aru Islands, but an occasional specimen has been taken in southern New Guinea. The spotted form, *rezia*, occurs all over New Guinea, abundantly, and reaches the Louisiade and D'Entrecasteaux Archipelagoes. Toxopeus (1950) says "There is . . . a rise running longitudinally through the Arapura sea and Torres Strait that links Aru with Merauke and Cape York, and which has a bearing upon the fauna of South New Guinea. In this respect it will suffice to point to the distribution of *Euploea usipetes*". Toxopeus does not agree with Zeuner's (*vide infra*) views of *Ornithoptera* and instead of dispersal via New Guinea in a very remote period suggests the connection via the Aru-Merauke ridge. *Papilio polydorus* of the *polydorus-orinomus-queenslandicus* section has a distribution like that of *usipetes*, from Aru through southern New Guinea to Sudest Island. The direct connection between the tail of New Guinea and Queensland has evidently existed independently of the Merauke-Aru ridge that linked Cape York with the Key Islands and so with the Southern Moluccas. Toxopeus states that "it is from Melanesia that in my opinion the bulk of the Papuan fauna (and its most typical part) may have

originated. The fauna of the western Pacific islands still shows many affinities to that of New Guinea". A striking disharmony, however, is provided by the *lewini* complex, which is such a feature of my "Fijian" area and is completely unrepresented from the Santa Cruz Islands north-westwards to New Guinea, and extremely scanty in those islands and New Hebrides.

The inter-relation of the Moluccas with the Solomons has been discussed at length by Zeuner (1943): there are certain *Euploea* which have a bearing on this question. Searching for the relations of the typically Solomons forms *boisduvalii* *fraudulenta* (No. 60, Pl. 2, fig. 5; Pl. 9, fig. 6), *phaenareta* *heurippa* (No. 118), and *nemertes* *polymela* (No. 128, Pl. 5, fig. 6), one finds the best match for them in the southern Moluccas. Thus *algea* Godart, 1819 (Pl. 9, fig. 2) of Buru and, in various forms, in the more northern Moluccas is the nearest to *fraudulenta* (*vide* previous notes in the taxonomy section under No. 60): *heurippa* is most nearly matched by *phaenareta* *hollandi* Fruhstorfer, 1930, from Buru, and perhaps even better by *cuvieri* C. & R. Felder, 1865, from Halmaheira, Gilolo, and Batchian, while the *phaenareta* species-complex has its centre in the Moluccas, six subspecies being listed by Hulstaert (1931). The *phaenareta* group was considered under taxonomy as subdivided into two sections, *callithoe* and *phaenareta* (Nos. 111 to 118). It is interesting, and relevant, here to note that in the Moluccas there are no forms of *callithoe*, which abounds in New Guinea, and is found in the Bismarcks, Waigeu, Jobi and Matty, and the Louisiade, D'Entrecasteaux, and Trobriand Archipelagoes, and that in the Solomons the whole group is represented from *phaenareta* stock.

As regards *polymela* it was pointed out in the taxonomic notes that *bernsteini* Felder, 1865, is more like *polymela* than any of the New Guinea forms, and *bernsteini* is a Moluccan subspecies.

Thus there are three cases among *Euploea* supporting the view put forward by Zeuner (1943) in his treatise on the distribution of *Troides* and especially the section *Ornithoptera* which developed mainly on the Moluccas and Solomons, although there are none on Buru. Zeuner says of *Schoenbergia* and *Ornithoptera*: "The two main groups must have separated early . . . and this differentiation appears to have been the consequence of the occupation of two parallel island rows. The northern island chain, from the northern Moluccas to the Solomons, became the home of *Ornithoptera*, and the southern chain, that of the Central Range of New Guinea, became the home of *Schoenbergia* . . ." [which remained in New Guinea]. The *Ornithoptera* group "clearly spread from the northern Moluccas (Halmaheira and possibly Ceram) where it developed . . . In the latest Pliocene an opportunity appears to have afforded itself to advance east to the Solomons, avoiding the Central Range of New Guinea". Zeuner points out certain difficulties in harmonizing the apparent age of the *Ornithoptera* with current views on the geology, and finds a way out of these difficulties by invoking "a moderate version of the theory of continental drift". On p. 173 we find the following: "According to this theory, the Australian block has been drifting northwards during and since the Tertiary . . . In the course of the Tertiary and the Pleistocene, the Australian block has moved north and, with its frontal portion, New Guinea, entered into and interfered with the island chains emanating

from Sundaland. In the past, therefore, New Guinea occupied a more southerly latitude than the northern Moluccas, and the incurving of the island chains around the Banda Sea is the result of New Guinea having been pushed into this alignment . . . A withdrawal of New Guinea out of the island chains towards the south-east, so that the Arfak Peninsula would lie approximately where now the centre of New Guinea is situated, would suffice to straighten out the disturbed island chains and *bring the northern Moluccas near to the Solomons*".

The three examples that have been given of the close relationship of Euploeas in Buru and the Solomons are in accord with this theory. A further interesting example is given by Lieftinck (1949B, p. 373). The Libellulid *Aethriamanta subsignata* Selys, previously only known from Buru and North Celebes, has now been found in the Solomons, two males having been taken on Guadalcanal. He says: "Curiously enough, our males of the Solomons correspond much more closely with the Moluccan *subsignata* than with the closely allied *nymphaeae* Lieft. of New Guinea". Of the Solomons Odonata in general Lieftinck says that they belong to Papuan or even to widely distributed genera. But the Chlorocyphid *Rhinocypha liberata*, recorded from Guadalcanal and Ugi belongs to an old complex of species within the genus having a very limited distribution in some islands of the southern Moluccas. It strongly resembles *R. ustulata* Brauer from Ceram and Ambon and *R. aurulenta* Först., from Buru. Lieftinck then refers to Zeuner's work on *Troides* and says that since *ustulata* is restricted to the *southern* Moluccas (whence *R. tincta*, which ranges from the northern Moluccas to New Georgia, is unknown) this example does not exactly correspond to Zeuner's hypothesis. Moreover *liberata* is confined to the easternmost islands of the Solomons, the others being occupied by sub-species of *tincta*. The relationship here is between the *southern* Moluccas and the Solomons, as with the three *Euploea* previously mentioned. Reference to the table of distribution of the Solomons *Euploea* (p. 134) shows that these three are widely distributed through the Archipelago, pointing to long residence there. Thus *fraudulenta* and *polymela* are both recorded for 20 islands, and the latter is the only truly Solomons form on Nissan, the most westerly of the Solomons, whose other two *Euploea* belong to the Bismarckian area. *Phaenareta heurippa* is recorded for 12 islands, like *honestia* and *nechos*, both well defined forms and probably old established: the highly peculiar *asyllus* is recorded from 14 islands. The only other form so universally distributed is *aenea*, which probably came from New Guinea.

A recent study by Belkin (1950) of the mosquitoes of the Solomon Isles has some points of interest for this paper. He considers that the Solomons "probably never were part of a continental land mass, as they are separated from neighbouring island groups by depths of ocean in thousands of feet, and even individual islands, although separated by narrow channels, are demarked by very deep water (see Lever, 1935, map). There is good evidence, in the form of coral ridges and plateaus on the large volcanic islands, that, in recent times, an uplift of about 1,500 feet has taken place. Thus, the Solomons are apparently oceanic islands that have derived their fauna and flora from the Papuan of New Guinea . . . We find that progressively the fauna, at least, becomes poorer and poorer as we go eastward. The sharpest reduction occurs between New Britain and New

Ireland, as a group, and the northern Solomons, . . . It appears . . . that in the genus *Troides* the Papuan element of New Guinea predominates in the Solomon Islands but has not played a prominent part in the population of the islands east of the Solomons. On the other hand the temperate Australian element has supplied more of the forms now known to occur in these islands and has even extended into the Solomon Islands". Belkin's remark about the sharp reduction between the Bismareks and the Solomons should be noted, with reference to the difference that has been pointed out between their respective *Euploea* faunas (p. 144). The writings of Ernst Mayr on the birds of the Pacific should be studied in detail. Two contributions to the Pacific Science Congress at San Francisco (1940) may be briefly extracted for the present study. He proposes a new definition for the *Polynesian region* to comprise "all the tropical and subtropical islands of the Pacific basin which indicate by their impoverished fauna that they have had no recent continental connection (after early Tertiary) and which derived the major part of their fauna directly or indirectly from the Papuan region, or jointly from Australia and the Papuan Region". Subdivisions are as follows.

(1) *Micronesia*. (Palau, Marianne, Caroline, Marshall and Gilbert Isles.) The bird fauna very poor, with a larger Palaearctic component than any other part of Polynesia: only Palau has more than eighteen species of land birds and shows strong Philippine influences (i). (This, with other numbers in brackets, refers to similarly numbered notes on the *Euploea* fauna at the end of the review of Mayr's conclusions.)

(2) *Central Polynesia*. (Fiji, Tonga, Samoa; Phoenix, Ellice, and Union Isles; Rotuna, Fotuna, Keppel, Niue, Niouafu, Uvea (Wallis Island).) The rich fauna shows the least pollution of Polynesian typical forms by recently arrived foreign elements: it is largely due to age and size of the chief Fiji Islands, which have 54 species, and Samoa 33 (ii); other islands are impoverished, Tonga having less than 20. Central Polynesia owes its zoogeographical character to the closeness of the three main components (Fiji, Samoa, Tonga) while wide spaces separate it from Micronesia and Eastern Polynesia. Mayr notes the two types of islands in central Polynesia:—

A. Old, big, mountainous with notable endemic fauna. In Fiji, Kandavu, Viti Levu, Ovalau, Vanua Levu, Taveuni, possibly also Ngau and Koro (iii). In Samoa, Upolu and Savaii.

B. Mostly coralline. Lau in eastern Fiji (iii), Tonga, Tutuila; Ellice, Union and Phoenix archipelagoes; Rotuna, Fotuna (iii), Niue, and Uvea (Wallis). Elements of the most typically Polynesian fauna that have developed in Fiji and Samoa have spread into Micronesia, Eastern Polynesia and Southern Melanesia (iv). Fiji being closer to the Papuan region received more immigrants from these either via the Solomons or Santa Cruz and New Hebrides: all the endemic elements belong to this fauna. A weak Australian element is a recent immigrant (v): most of them are absent from the Solomons but are found in New Hebrides so that it seems that they reached Fiji only after the New Hebrides had emerged to serve as a stepping stone. Only one (a forest dweller) reached Samoa; none reached Tonga.

(3) *Eastern Polynesia*. All islands east of 165° W. (Society, Tuamotu, Marquesas, Cook, Austral and "Line" Islands). Extremely poor fauna showing a high degree of slight endemism, but a low degree of strong endemism: 17 species is the maximal number for any one island (Tahiti). Cook Islands have a slight central Polynesian element (vi).

(4) *Southern Melanesia*. (Santa Cruz, Banks, New Hebrides, New Caledonia, Loyalty Isles.) Santa Cruz is a young group without endemic genera and only three endemic species: there are more elements from New Hebrides than from Fiji, and more from Fiji than from Solomons (vii). In the Banks group and New Hebrides (the Torres group has very poor bird fauna) the Papuan element is stronger than in New Caledonia (viii). Low degree of endemism and strong Australian influence. The fact that some Papuan species of New Caledonia do not occur in New Hebrides, speaks against high age and continental connection. The Banks Islands have very much the fauna of the northern New Hebrides (Santo group) (ix). The three (ix) southern islands of New Hebrides lack most of the endemic species and genera and show relationship with the Loyalties. New Caledonia apparently emerged in the Oligocene and has remained alone. Australian and Papuan influence equally strong, the former prevails amongst more recent elements, the Papuan amongst the older (viii). The Loyalties are younger than New Caledonia, and probably had no connection with it, being on a different arc. The bird fauna more resembles that of the New Hebrides than of New Caledonia, but Papuo-Melanesian influence is stronger than in New Caledonia. Mayr places *Northern Melanesia* in the Papuan subregion: it includes the Admiralty, Bismarck, and Solomon Islands. He comments on particularly interesting conditions on San Cristobal (*vide* pp. 133-5): there are probably half-a-dozen species which were blown to that island by the S.E. trade wind from somewhere in southern Melanesia or central Polynesia, but which have not succeeded in going any further. These strays are particularly characteristic of marginal areas and do not form a significant part of eastern Polynesia.

- (i) It would be interesting to know whether there is any bird comparable with the strangely isolated *abjecta* (No. 53, of the *algea* complex) on Palau, or with No. 52, *eleutho*, on Guam.
- (ii) Fiji has eight forms of *Euploea* (omitting Fotuna, Wallis, and Ellice Islands, not included in Fiji by Mayr) and Tonga only one.
- (iii) From all these old islands *walkeri* (No. 9) is absent whereas it is widely distributed in Lau and present on Fotuna and the Ellice group. (Compare the notes on Fijian *Euploea*, p. 142.)
- (iv) *e.g.*, *lewinii brunnescens* and *l. lilybaea*, Nos. 1 and 2.
- (v) *cp. tulliolus*, No. 96.
- (vi) *cp. lewinii perryi*, No. 10.
- (vii) Santa Cruz and Solomons groups.

There are fifteen named forms of *Euploea* on the Santa Cruz Islands, which I allot as follows according to their derivation. From Solomons nine, *e.g.*, No. 60, *fraudulenta*, No. 62, *brenchleyi*, No. 64, *era*, No. 65, *lapeyrousei*, No. 66, *matemae*, No. 89, *viridis* trans. to *jessica*, No. 91, *aenea*, No. 128, *polymela*, No. 131, *crucis*. From the "Fijian" area four, *e.g.*, No. 1, *brunnescens*, No. 78, *tristis*, No. 132,

eustachiella, No. 133, *iphianassa*. From the "Papuasian" area, two, *e.g.*, No. 75, *moesta*, No. 76, *melander*.

(viii) The *Euploea*, as plotted below, do not show a great Papuan superiority in Banks and New Hebrides, compared with New Caledonia.

BANKS AND NEW HEBRIDES.		NEW CALEDONIA.	
"Papuasian"	"Fijian"	"Papuasian"	"Fijian"
or, at least, Solomons		or, at least, Solomons	
No. 64. <i>era</i>	No. 2. <i>lilybaea</i>	No. 54. <i>helcita</i>	No. 3. <i>montrouzieri</i>
No. 67. <i>torvina</i>	No. 96. <i>tulliulus</i>	No. 69. <i>rileyi</i>	No. 78. <i>tristis</i>
No. 68. <i>bakeri</i>	No. 98A. <i>forsteri</i>	No. 90. <i>jessica</i>	No. 96. <i>tulliulus</i>
No. 76. <i>melander</i>	No. 77. <i>magnipunctata</i>	No. 133. <i>iphianassa</i>	No. 98A. <i>forsteri</i>
No. 90. <i>jessica</i>	No. 78. <i>tristis</i>		No. 99. <i>adyte</i>
No. 133. <i>iphianassa</i>			
No. 134. <i>novarum-ebudum</i>			

(ix) The three southern isles are Erromanga, Tana, and Aneityum. The knowledge of *Euploea* from the first is inadequate: the two latter have No. 67, *torvina* (probably of Solomons or Santa Cruz ancestry), and Nos. 96 and 98, forms of *tulliulus* (probably of Fijian or Australian ancestry) not present in the northern islands.

PART 6. SOME ANOMALIES IN DISTRIBUTION.

It is generally acknowledged that the island fauna of the Pacific, at least as regards butterflies, and especially *Euploea* as I pointed out earlier, has been derived from the north west. In other words, *Euploea* had considerable powers of dispersal: if this was the case in the past there seems no reason why it should not still be so. These butterflies are known to move in large companies, though whether this is true "migration" has yet to be proved. At any rate a number of cases are recorded by Williams (1930), and in the account of the *Euploea* of Samoa will be found an observation on flight over the sea. I have thought it interesting to gather together records of anomalous distribution from specimens seen by myself: it will at least show that they have been noticed, and will emphasize the need for confirmation in the future. Some, of course, seem at present merely to be an example of mistaken or careless labelling. A good example is the type of *usipetes usipetes*, No. 136, which purports to come from Port Moresby in New Guinea. This has been questioned by that extremely careful and accurate worker, the late A. S. Corbet. Yet, during my examination of every specimen I could find, I came across another male specimen from Port Moresby, one from Ekeikei, and one female from Yule Island. Other specimens that I saw were all from Aru, totalling 34. Under *tulliulus*, No. 96, will be found some other suggestive facts. The following are therefore given without any attempt to justify them.

No. 1, *brunnescens*, one male from Guadalcanal. No. 4, *eschschooltzii*, one male, one female, from Anuta (Anuda) Island. No. 3, *montrouzieri*, one male from Dolphin Island. No. 11, *doretta*, two males from Guadalcanal, coll. Webster. No. 19, *cerberus*, two males from New Georgia, coll. Webster. No. 23, *eboraci*, two males from German New Guinea. No. 58, *prusias*, from Aola, Guadalcanal.

coll. Woodford. No. 59, *pronax*, one male from Guadalcanal. No. 67, *torvina*, from Mallicolo. No. 80, *sylvester*, two males and one female from Port McQuarie. No. 93, *asyllus*, ex Oberthür, from Dorey Bay, New Guinea. No. 96, *tulliolus*, ex Felder, from New South Wales. No. 102, *pyres*, one from New Guinea. No. 103, *mangolinella*, one female from New Georgia. No. 108, *bismarckiana*, two males from Shortlands, coll. Ribbe. No. 126, *perdita*, one from New Georgia, coll. Webster. No. 128, *polymela*, one male from Santa Cruz. No. 133, *iphianassa*, from Bougainville.

PART 7. WHITE BORDERED FORMS AND MÜLLERIAN ASSOCIATIONS.

It was the curious prevalence of white-bordered forms in some of the Solomon Islands which led to the investigations now recorded in this study. De Nicéville & Kühn (1898) allude (p. 254) to the prevalence of white marked *Euploea* and their mimics on the Ké Islands. Talbot (1921) drew attention to "mimetic groups" and published illustrations of white-bordered associations from the Kei and Aru Islands. He also discussed the likenesses between various "species" in other areas, including those of Fiji which Poulton (1923) discussed in detail, and of Australia. Talbot concluded "The larger the body of observed facts which are consistent with a hypothesis supported by such evidence in other areas, the greater the probability that the hypothesis is valid".

There could hardly be better, though indirect, evidence than that set forth in the table (p. 134) dealing with the Solomon Islands. With few exceptions, which indeed have a bearing on the argument, the normal and white-bordered representatives of subspecies mutually replace each other. The facile suggestion that this is due to similar environmental influences does not stand up to closer examination. Thus, the white-bordered form *pyrgion*, of *boisduvalii*, characteristic of Malaita, occasionally occurs on Guadalcanal and Florida, in the presence of the usual *fraudulenta*. Again, *brenchleyi* which is so typical of San Cristobal at the extreme south-east end of the Solomons, has also been taken on Bougainville at the extreme north-west end. It seems odd, to say the least, that the normal *nechos*, widely distributed through the Solomon Islands, great and small, and offering different conditions without any effect, should be so peculiarly affected by the conditions on Malaita that it becomes a white-bordered form *pronax*, and by the conditions of San Cristobal and its small neighbours so that it becomes a slightly different white bordered form *prusias*.

There seems to be a widespread tendency in *Euploea*, especially the females, to vary towards paler margins, as in *novarum-ebudum*, and this may become a definite white border. The aberration of *macleayi* from Fiji, shown on Pl. 9, fig. 4, is an extreme case. A remarkable example of whiteness, in which the whole wings are white above and below, is the form *browni* of *unibrunnea*: the intermediate, pale brown form *majuma* is extremely rare, whereas *browni* seems to be common. This white form occurs only in the Bismarek Archipelago together with *unibrunnea*, and such a form never occurs in the closely allied *heurippa* of the Solomons. If some dominant *Euploea* on an island produced a mutant white bordered form which could maintain itself, it might gain by being more conspicuous and better able to advertise its distastefulness. It might

replace the normal, duller, parent form, and it might be advantageous to other *Euploea* on that island to develop their own tendency towards paler margins into an actual white border, and thus develop an association such as occurs on Malaita and San Cristobal. On Malaita *pyrgion* seems predominant, and associated with it are *woodfordi* and *pronax*, of widely different groups and less common, and *gerion* of yet another group and at present only known by one male and one female, although a total of 123 specimens of *Euploea* has been recorded from Malaita. San Cristobal and its small neighbours are equally interesting. The most numerous white-bordered form is *brenchleyi* and associated with it, but less abundant, is *imitata*: *prusias* is still less abundant while *albomarginata* is very rare indeed and *leucacron* only known by two specimens. These last two may well be recent developments. The total number of *Euploea* from San Cristobal and the small neighbours on which these white bordered forms occur is 210. The fact that other butterflies on these islands have adopted white borders (e.g., *Danaus philene insolata* Butler on San Cristobal and Santa Ana) is very suggestive.

The question naturally occurs: Has the very large and completely white *browni* had any influence in the Bismarck Archipelago? Curiously enough, it has had none upon other *Euploea*, for it is unique in that area. Again, it may be asked: Why has not a white border developed more often in Fiji, from such a beginning as is shown on Pl. 9, fig. 4? This cannot at present be answered. The evidence does suggest that the white border is due to "internal" rather than "external" causes, but that once it is produced it may, by causing greater conspicuousness, favour the development of a race which may replace the original form and influence other species to develop their own paler borders.

Rennell Island, of which the *Euploea* fauna has been unknown until now, furnishes another example of similarity between forms of different groups. It appears, from the collection made by the Templeton-Crocker Expedition, that a very well defined form of the *core* complex, unknown elsewhere, is common there: its effect is reinforced by a similarly marked form of the *batesii* complex derived from a common New Guinea form. The form of *nemertes* so abundant in the Solomons, has been modified on Rennell into an unusually heavily white-marked form, new to science, resembling the other two in general appearance. Only a single specimen of this is known, and a large collection of *Euploea* on Rennell, made without selection, would be of absorbing interest. (See Addenda.)

Lastly, the peculiarity of the *Euploea* of St. Mathias Island at the eastern edge of the Bismarck Archipelago, is fitly mentioned here; in this case it is difficult to think that the coloration is more conspicuous. Five forms of *Euploea* are known, and the total number of specimens seen from St. Mathias is seventy-two. There are two forms of the *treitschkei* complex, and the following three: No. 21, *cerberus griseitincta*; No. 48, *illudens mathiasana*; and No. 127, *nemertes pulchella*. Reference to the taxonomic section will show that for each of these three there is a note on the unusual greyish tint of the ground colour towards the apex of the F.W.

PART 8. ACKNOWLEDGMENTS.

Firstly, to Mr. N. D. Riley, C.B.E., Keeper of Entomology at the British Museum (Nat. Hist.), for allowing me complete freedom in examining the

collections in his charge at South Kensington and Tring, and in selecting specimens for photography. Thus it has been possible to survey the material collected by Godman and Salvin, Lord Rothschild, Oberthür and Fruhstorfer. All this, with the great collection in the Department of Entomology of the University Museum at Oxford under the Hope Professor, who kindly allowed me undisturbed use of a room, has provided most of the material. Next, I would thank Dr. Edward S. Ross, Curator of Entomology, California Academy of Sciences, for his great kindness in sending over to me the whole of the *Euploea* collected by the Templeton-Crocker expedition on Rennell and other islands in the Solomons. Curators of collections elsewhere have been most helpful in sending specimens for examination. In America, Dr. James H. McDunnough, Dr. Herbert F. Schwarz and Dr. Frederick H. Rindge of the American Museum of Natural History, and Dr. Austin Clark of the United States National Museum. In Australia, the directors of the Australian Museum and the South Australian Museum. In Paris, Monsieur Jules Bourgogne was most kind in searching for the elusive type of Montrouzier's "*vitella*" and sent me also specimens for examination, and Monsieur P. Viette supplied an answer to a query. Dr. Sharp sent me *Euploea* from the Cambridge Museum, and the curators of entomology in the museums of Birmingham, Newcastle and Edinburgh allowed me access to their collections by which some useful records were obtained. Heer F. Bryk was most helpful when I visited the Stockholm Museum, and Dr. K. Jordan, F.R.S., and Mr. F. Goodson at Tring, have kindly dealt with enquiries as did Mr. A. G. Gabriel at South Kensington. In 1938 Dr. Martin Hering kindly sent some specimens from the Berlin Museum for identification. Professor H. Boschma of the Rijksmuseum, Leiden, and Professor John Belkin of the University of California were written to, with satisfactory results, also Mr. C. A. Gibson-Hill of the Raffles Museum, Singapore. Mr. P. F. Mattingly and Miss E. Marks introduced me to the distribution of mosquitoes and Lt. Cdr. K. L. Knight of U.S. Naval Medical Research Unit 3, kindly sent much information, but it has not been practicable to include a study of this subject. At Oxford, Dr. B. M. Hobby spent much time in putting into order the beginnings of a troublesome bibliography, and Mr. E. Taylor, Senior Laboratory Assistant prepared many genitalia for me. The Hope Professor kindly allowed a great deal of help from his clerical staff especially Mrs. Audrey Smith. Finally, the splendid material from Fiji and the Solomons, sent to Oxford by Mr. H. W. Simmonds and Mr. R. J. A. W. Lever must be especially mentioned, as it is unrivalled, even at Tring and South Kensington as a representative collection of the *Euploea* fauna of most of the islands.

PART 9. SUMMARY.

(1) A total of 9,142 specimens, comprising 137 named forms, is discussed: many others were discarded for inadequate data.

(2) Eleven new forms are described.

(3) The area described by the title is considered under the following subdivisions according to the character of the *Euploea* fauna.

(A) *Bismarckian*.

(1) Admiralty Islands; (2) Bismarck Archipelago.

(B) *Papuanian*.

- (1) Vulcan Island ; (2) Dampier Island ; (3) Louisiade Archipelago, including Rennell Island in the Solomons ; (4) D'Entrecasteaux Archipelago ; (5) Trobriand Archipelago.

(C) *Solomons*.

- (1) Bougainville and the British Solomon Islands Protectorate ;
(2) Santa Cruz group.

(D) *New Hebridean*.

- (1) Torres Isles ; (2) Banks Isles ; (3) New Hebrides.

(E) *New Caledonian*.

- (1) New Caledonia ; (2) Loyalty Islands.

(F) *Australian*.(G) *Fijian*.

- (1) Fiji, with Wallis Island and Ellice group ; (2) Tonga ; (3) Niue ;
(4) Samoa ; (5) Union Island ; (6) Cook Islands ; (7) Tahiti.

(H) *North Pacific (Micronesia)*.

- (1) Palau ; (2) Mariannes.

(4) The Bismarckian fauna is so distinct from that of the Solomons that it seems unlikely that the latter obtained their *Euploea* via the Bismarcks.

(5) Rennell Island, geographically in the Solomons, is more closely related to the Papuanian area (Louisiades) than to the Solomons.

(6) Certain similarities between the fauna of the Moluccas (especially Buru) and the Solomons support a theory of continental drift.

(7) The distribution of Pacific *Euploea* accords well with that of birds as established by E. Mayr.

(8) The mysterious "*vitella*" of Montrouzier is most probably *boisduvalii fraudulenta* Butler, 1882.

(9) *E. lapeyrousei* has been a source of much confusion. Oberthür associated with Boisduval's female type, which is a small form of *boisduvalii* from Vanikoro, a male of quite another species (*netscheri* Snellen, 1889) which has long been accepted as the allotype of *lapeyrousei*.

(10) The white bordered forms on Malaita and San Cristobal in the Solomons are considered to be due to synaposematic resemblance. Two new members, and the previously unknown male of another, are described.

(11) A series of tables gives for each form the maximal and minimal development of the spot pattern by which a future change can be estimated.

ADDENDUM, MAY 28, 1952.

After the completion of this account I have been privileged to see a collection of *Euploea* from Rennell Island made in 1951 by the Danish expedition on the "Galathea". An appeal to the Zoological Museum of Denmark by the Keeper of Entomology at the British Museum, on my behalf, was most generously received and the specimens were sent to me for study in May. I am exceedingly grateful

for this kindness, for the 35 *Euploea* (all males) most interestingly bore out the conclusion derived from the almost similar number collected by the Templeton-Crocker expedition. There were also 11 Danaines, but none of the normal dark *Euploea* so abundant in the Solomon Isles.

E. core rennellensis, as before, predominated with 32, all males. As before they showed remarkably little variation, and the species must have been very long isolated. No differences on the upper surface were seen as compared with the former specimens: the underside of the fore-wing of one showed the short discal streak in area 2 to be strongly bifurcate externally.

A single male of *E. batesii kunggana* resembled the holotype above: on the underside there were the following slight differences. F.W., admarginals, only a pair in 5 attached to end of submarginals, and one of a pair in 6, similarly. Submarginals 1-9. The only discal was a clear small spot in 3.

Two male *E. nemertes rossi* were most welcome, as only the holotype had previously been seen; their spotting differed in the following slight respects from that of the type: (a) F.W. underside. D.10 only a faint trace; (b) F.W. upper side. The pair of admarginals in 1b not fused; no trace of S.9. H.W. upper side. S.6 minute. Underside, F.W., admarginals, only trace of pair in 1b; pair 2 faintly linked to S.2, pairs 3-6 small. H.W. the double row made by the admarginals and submarginals is poorly developed: the admarginals are small and not so intimately linked to the submarginals, which are also small, as in the type, the linkage is shown feebly in areas 1c, 2, 3.

G.D.H.C.

SECOND ADDENDUM, JULY 16, 1952.

A small additional set of seven *Euploea* reached me at the end of June, and proved to be of great interest, as the specimens were *females*, not previously seen. Again, none of the common dark forms of the Solomons were represented and the question arises whether the two *fraudulenta* and one *brenchleyi* may not have been wrongly labelled.

Dr. Wolff wrote to me with the second consignment: "Regarding the dark and little spotted species which is in the Californian Museum I can only say that my assistant and I tried to collect all that we saw. We always moved around with a butterfly-net and not very much escaped us. Butterflies on Rennell are scarce except for the form of *core*". The present supplementary collection contained two battered males, and three of the previously unknown females, one of which is taken as *Allotype*. It bears data "L 366. 18.x.1951. Regenskoo V. Tevarmangu". Slight differences from the *Holotype* are as follows. Upper side, F.W., a pair of submarginals in 1b. H.W., admarginals, single 1b, pairs 1c-4 joined to submarginals: anterior one of pair in 5 free: small 6. Underside, admarginals, posterior of pair in 2 very small. Discals, faint streak in 1b, small 2-3. H.W. as on upper side. As compared with the two paratype females, submarginals, 1b on F.W. are rather undeveloped, and do not form one large spot.

Paratype ♀ A. L 384. 22-23.x.1951. Niupani, Tenggano, has minor differences as follows: Above, F.W. submarginals 1b almost form one large spot. H.W. pair

submarginals in 5 joined to admarginals. Below, F.W. trace pair admarginals in 2. Discals trace streak 1b: small 2-3, trace 5.

Paratype ♀ *B*, same data. F.W. venation irregular: area 6 expanded, pushing vein 7 forwards, area 8 not clear, no spots. H.W. also a little irregular, margin of spot in 3 abnormal. F.W. has no discal streak, or spots, below. The submarginals rather larger than in the other specimens.

E. nemertes rossi ♀ allotype. L 384. 22-23.x.1951. Niupani, Tenggano. Differs little from Holotype, except that on F.W. in 1b the absence of the brand leaves room for a pair of admarginals joined to a submarginal. Traces of admarginals 2-5. Submarginal 9 very small. D.10 just visible as a few scales. H.W. like that of Holotype. Underside, F.W. Single admarginal in 1b joined to S, pairs 2-6, single 7: in 2 they are faintly joined to submarginal 2. Submarginals, pair 1b incompletely fused: joined to anterior admarginals: 2-8. Discal on right side only is visible a small, circular, bluish white 2. Trace of bluish spot in 6, at 10 a few scales. H.W. as on upper side, but pair in 5 free from S.5: S.6 small and circular.

E. batesii kunggana ♀ paratype. L 366. 18.x.1951, Regenskoo V. Tevannangu. Following should be noted: Above: F.W. as allotype. H.W. Proximal spot 1b almost absent. Area 6, left side, only the posterior admarginals. Below: F.W. Admarginals minute and irregular. Submarginals 1b-8, trace 9. Discal single streak in 1b. H.W. Discal minute 2-6.

G.D.H.C.

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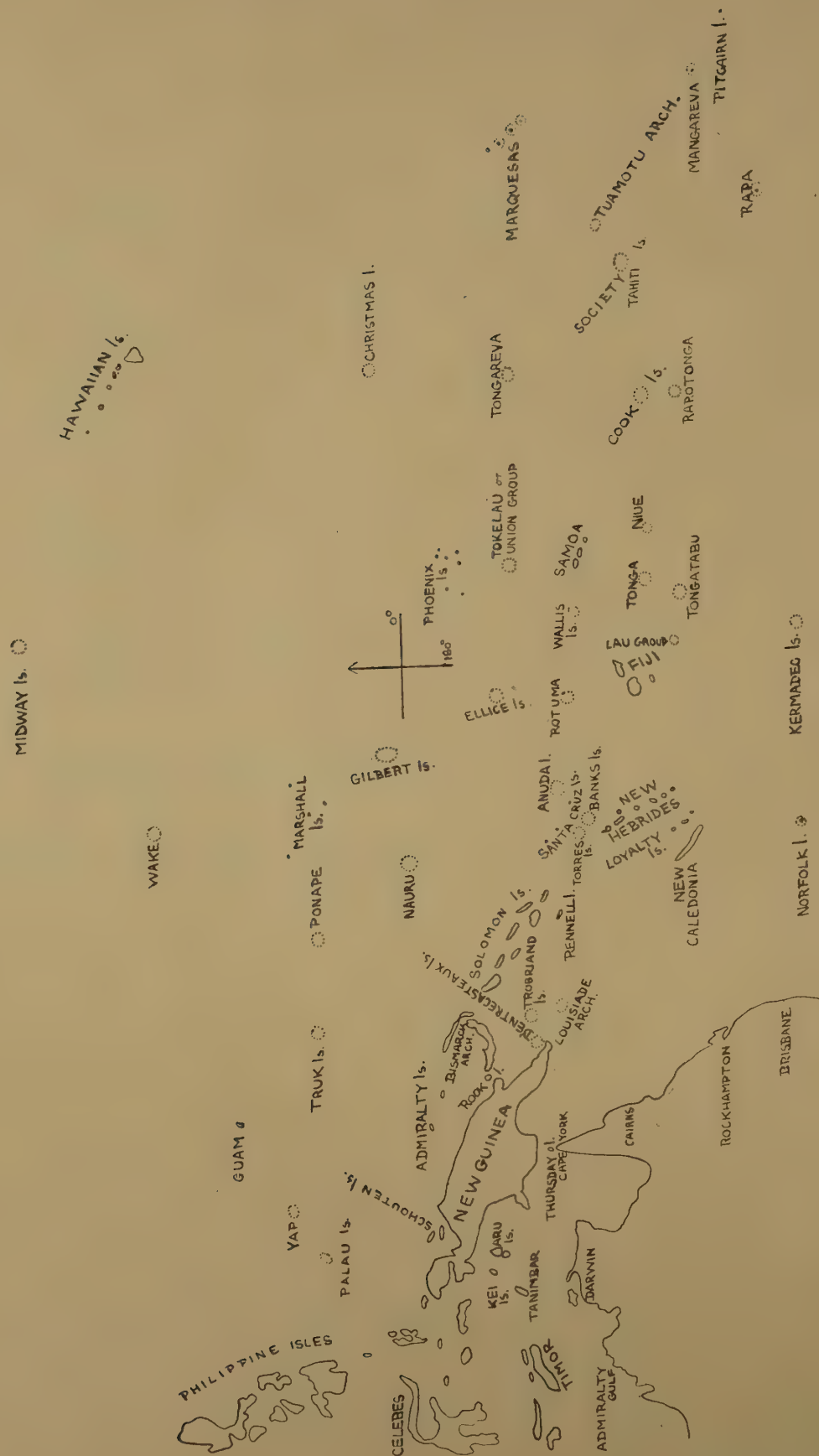


PLATE 1.

PLATE 1.

Origin of spot pattern.

- Fig. 1. *Danaus similis exprompta* Butler, 1874. Male. North Central Ceylon, Ratanpura. W. Ormiston, July, 1921.
- Fig. 2. *Euploea gelderi dongo* Doherty, 1891. Female. Sumbawa, Tambora.
- Fig. 3. *E. euctemon* Hewitson, 1866. Female. North Celebes, Minahassa.
- Fig. 4. *E. horsfieldii kirbyi* C. & R. Felder, 1865. Female, underside. North Celebes, Minahassa, Tondano, June–July, 1899.
- Fig. 5. *E. asyllus asyllus* G. & S., 1888. Solomon Isles, Guadalcanal, Aola. C. M. Woodford.
- Fig. 6. *E. mulciber mulciber* Cramer, 1777. Female. Penang. Bourke.
- Fig. 7. *E. redtenbacheri malayica* Butler, 1878. Female. Sumatra. A. R. Wallace, 1871.

All specimens in the University Museum, Oxford. This and the other photographs by H. F. Woodward of the Department of Forestry, Oxford.



The genus *Euploea* (Lepidoptera—Danaiidae).

PLATE 2.

PLATE 2.

Peculiarities of spotting, on underside.

- Fig. 1. *E. l. lewinii* C. & R. Felder, 1865. Female. Tonga, Tongatabu, G. H. E. Hopkins, March 7, 1925. Shows the large spot in F.W. area 3.
- Fig. 2. *E. lewinii brunnescens*, subsp. nov. Male paratype. Santa Cruz Isles, Vanikoro, November 17, 1927. Shows F.W. D.3 embraced by S.3.
- Fig. 3. *E. lewinii distincta* Butler, 1874. Male. Niue Island, H. W. Simmonds, October 21, 1939. Shows F.W. D.3 almost engulfed by S.3.
- Fig. 4. *E. lewinii walkeri* Druce, 1890. Female. Fiji, Suva, at ship's light, L. H. Mosse-Robinson, May-July, 1908. Shows in F.W. area 2, the same as in area 3 in the last two specimens.
- Fig. 5. *E. boisduvalii fraudulenta* Butler, 1882. Solomon Islands, Vella Lavella, R. J. A. W. Lever, September 15, 1936. Shows on F.W. the large bar formed by D.2 joining with the two spots of submarginal series making a forked extremity as in "*vitella*".
- Fig. 6. *E. boisduvalii mangoensis* Butler, 1884. Male. Fiji Lau, Thithia, H. W. Simmonds, August 31, 1921.
Note small size of F.W. D.2.
- Fig. 7. *E. sylvester tristis* Butler, 1866. Female. Torres Islands, Tegua, J. J. Walker, September 14, 1900. Shows full spotting, with an accessory to H.W. cell-spot.

All specimens in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera – Danaidae).

PLATE 3.

PLATE 3.

Forms of *Euploea treitschkei* Boisduval, 1832.

- Fig. 1. *E. t. gaedei* Bryk, 1937. (= *olivacea* Grose Smith, 1894.) Male. Schouten Isles, Biak, A. C. and F. Pratt, June, 1914. A short-winged specimen. H.W. spots only D.2.3, minute 4, 5.6 (Cell)+.
- Fig. 2. *E. t. viridis* Butler, 1882. Male. A long-winged specimen. "New Guinea" H.W. spots, (S). 1c, pair 2 joined to D.2, small pair 3, 4-6 (D). Pair 2 joined to S.2, 3, minute 4.5, 6. (Cell). Faint trace.
- Fig. 3. *E. t. aenea* Butler, 1882. Female. Solomon Islands, Guadalcanal, Aola, C. M. Woodford, 1887. H.W. spots. (S) 1c joined to D.1c, pair 2 joined to D.2 making a horseshoe, 3, 4 joined to D.4, 5.6. (D) 1c joined to S.1c, 2 to S.2, 3, 4 joined to S.4, 5.6.7. (Cell)+.
- Fig. 4. *E. t. viridis* Butler, 1882. Female. D'Entrecasteaux Archipelago, Goodenough, D. J. Jenness, April, 1912. H.W. shows commencement of large patches by fusion of Submarginals with Discals.
- Fig. 5. *E. t. caerulea* Ribbe, 1898. Male. New Britain, Webster, 1894. The ground colour of this and Nos. 6-8 is deep rich blue. This specimen shows the small beginnings which develop through 6-7 into the large white areas of 8.
- Fig. 6. *E. t. lorenzo* Butler, 1870. Male. Banks Islands, Pakea, H. W. Simmonds, November 27, 1923. Increase of suffusion around F.W. spots. Except for this the specimen is like Butler's type.
- Fig. 7. *E. t. jessica* Butler, 1869. Male. New Hebrides, Malekula, J. J. Walker, July, 1900. Butler's type differs by lacking the dyslegnic streak in F.W. cell, and in area 1b the markings are not quite so large.
- Fig. 8. *E. t. erimas* G. & S., 1878. Male. New Hebrides, Mai Islet, P. A. Buxton, June 22, 1928. The type of *erimas* came from New Ireland (*cp.* No. 5 above). All F.W. spots have coalesced. There is a similar female from Mai at Oxford.

All specimens in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera—Danaiidae).

PLATE 4.

PLATE 4.

New or little known forms of *Euploea*.

- Fig. 1. *E. alcatheae samaraina* Mihi. Male holotype. Samarai Island at eastern end of Papua. Adams bequest, British Museum (Nat. Hist.).
- Fig. 2. *E. boisduvalii lapeyrousei* Boisduval, 1932. Male ne-allotype. Santa Cruz Islands, Vanikoro. R. J. A. W. Lever, May-June, 1933.
- Fig. 3. *E. boisduvalii matemae* mihi. Male holotype. Santa Cruz Isles, Matema. M. W. Hows, Jr. for Templeton-Crocker expedition, July 9, 1933.
- Fig. 4. As last. Female allotype.
- Fig. 5. *E. jennessi* Carpenter, 1942. Male holotype. D'Entrecasteaux. Archipelago, south-east of Goodenough Island, near Bwaidoga. D. Jenness, February, 1912.
- Fig. 6. *E. boisduvalii lapeyrousei*. Female, similar to holotype. Santa Cruz Isles. Vanikoro, R. J. A. W. Lever, May-June, 1933.
- Fig. 7. *E. sylvester magnipunctata* Carpenter, 1942. Male holotype. Banks Islands, Ureparapara, J. R. Baker, Sept. 30, 1922.
- Fig. 8. Do. Female allotype. Banks Islands, Pakea. H. W. Simmonds, November 27, 1923.

No. 1 in British Museum (Nat. Hist.).

Nos. 3, 4 in California Academy of Sciences.

Nos. 2, 5, 6, 7, 8 in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera—Danaiidae).

PLATE 5.

PLATE 5.

Rennell Island novelties.

- Fig. 1. *E. batesii kunggana* mihi. Male holotype. Rennell Island, Kunggana Bay. Templeton-Crocker expedition, M. Willows, junior, June 6, 1933.
- Fig. 2. *E. core rennellensis* mihi. Male holotype. As 1, but June 14.
- Fig. 3. *E. nemertes rossi* mihi. Male holotype. Date as for 2.
- Fig. 4. *E. kunggana*. Female allotype. As 1.
- Fig. 5. *E. batesii resarta* Butler, 1876. Male. For comparison with 1. Louisiade Archipelago, Nivani Island, G. M. Carson, April 5, 1912.
- Fig. 6. *E. nemertes polymela* G. & S., 1888. Male. For comparison with 3. Guadalcanal, R. J. A. W. Lever, February-March, 1932.

Nos. 1-4 in the museum of the California Academy of Sciences.

Nos. 5-6 in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera-Danaidae).

PLATE 6.

PLATE 6.

Specimens of forms of *Euploea* usual in the Solomons.

- Fig. 1. *E. batesii honesta* Butler, 1882. Male. Guadalcanal. R. J. A. W. Lever, February–March, 1932.
- Fig. 2. *E. nechos nechos* Mathew, 1887. Male. New Georgia.
- Fig. 3. *E. boisduvalii fraudulenta* Moore, 1882. Male. Tulagi. H. W. Simmonds, September 21, 1923.
- Fig. 4. *E. asyllus asyllus* G. & S., 1888. Shortlands, Alu Island. C. M. Woodford, June 23 to mid-August, 1886.
- Fig. 5. *E. honesta*, female. Guadalcanal.
- Fig. 6. *E. nechos*, female. Rubiana. C. M. Woodford.
- Fig. 7. *E. fraudulenta*, female. Shortlands, Faisi. H. W. Simmonds, October 2, 1923.
- Fig. 8. *E. asyllus*, female. Guadalcanal. C. M. Woodford, March 30 to September 25, 1887.

No. 6 in the British Museum (Nat. Hist.).

All others in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera—Danaiidae).

PLATE 7.

PLATE 7.

White-marked forms of *Euploea* from Malaita, Solomon Islands.

- Fig. 1. *E. woodfordi* G. & S., 1888. Male. C. M. Woodford.
Fig. 2. *E. nechos pronax* G. & S., 1888. Male. C. M. Woodford.
Fig. 3. *E. boisduvalii pyrgion* G. & S., 1888. Male. C. M. Woodford, May, 1886.
Fig. 4. *E. asyllus gerion* G. & S., 1888. Male ne-allotype. M. Hows Jr., for Templeton-Crocker expedition, May 26, 1933.
Fig. 5. *E. woodfordi*. Female. R. J. A. W. Lever, January, 1932.
Fig. 6. *E. nechos pronax*. Female allotype. C. M. Woodford.
Fig. 7. *E. boisduvalii pyrgion*. Female. C. M. Woodford, May, 1886.
Fig. 8. *E. asyllus gerion*. Female type. C. M. Woodford.

Nos. 1, 6, 8 in British Museum (Nat. Hist.).

No. 4 in California Academy of Sciences.

Remainder in University Museum, Oxford.

Photographs Nos. 6 and 8 by the kindness of the Keeper of Entomology, British Museum (Nat. Hist.).



The genus *Euploea* (Lepidoptera - Danaidae).

PLATE 8.

PLATE 8.

White bordered forms of *Euploea* from the eastern Solomon Islands.

- Fig. 1. *E. batesii leucacron* mihi. Male paratype. "Australasia." Leggett, 1902 (? Ugi). British Museum (Nat. Hist.).
- Fig. 2. *E. nechos prusias* G. & S., 1888. Male. Santa Ana Island. R. J. A. W. Lever, October, 1932.
- Fig. 3. *E. boisduvalii brenchleyi* Butler, 1870. Male. San Cristobal Island, Waimamuru. R. J. A. W. Lever, May 10, 1935.
- Fig. 4. *E. nemertes imitata* Butler, 1870. Male. Santa Ana Island. R. J. A. W. Lever, October, 1932.
- Fig. 5. *E. boisduvalii albomarginata* mihi. Female holotype. San Cristobal Island, A. S. Meek, April 19 to May 9, 1908. British Museum (Nat. Hist.), Tring.
- Fig. 6. *E. nechos prusias* G. & S., 1888. Female ne-allotype. Ugi. Woodford. British Museum (Nat. Hist.), Tring.
- Fig. 7. *E. brenchleyi* Butler, 1870. Female. San Cristobal Island, Waiai. R. J. A. W. Lever, May 8, 1935.
- Fig. 8. *E. nemertes imitata* Butler, 1870. Female. Santa Ana Island. R. J. A. W. Lever, October, 1932.

All specimens except Nos. 1, 5 and 6 in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera - Danaidae).

PLATE 9.

PLATE 9.

- Fig. 1. *E. sacerdos* Butler, 1883. Male. Tenimber, W. Doherty, 1892.
Fig. 2. *E. algea* Godart, 1819. Male. Buru, W. Doherty.
Fig. 3. *E. tulliolus arisbe*, C. & R. Felder, 1865. Male. Timor, Godman-Salvin colln.
Fig. 4. *E. nemertes macleayi*, C. & R. Felder, 1865. Female, a remarkable aberration, with well developed white border. Fiji Lau, Lakemba, R. J. A. W. Lever, November 8, 1945.
Fig. 5. *E. algea reginae* subspecies nov. Male holotype. N.W. Australia, Queen's Island, J. J. Walker, June, 1890.
Fig. 6. *E. boisduvalii fraudulenta* Butler, 1882. Male. Solomon Isles, Tulagi, H. W. Simmonds, October 13, 1923.
Fig. 7. *E. tulliolus niveata* Butler, 1875. Queensland, Godman-Salvin colln.
Fig. 8. *E. nemertes assimilata* C. & R. Felder, 1865. Female. Key Islands, W. J. C. Frost, January-March, 1916.

Nos. 1, 2, 3, 5, 7 in the British Museum (Nat. Hist.).

Nos. 4, 6, 8 in the University Museum, Oxford.



The genus *Euploea* (Lepidoptera—Danaiidae).

The caecum of monotremes and marsupials.

By

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(With Plates 1-8 and 3 figures in the text.)

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INTRODUCTION.

In a previous memoir (Hill & Rewell, 1948) the morphology of the caecum was considered through the Primate series. A number of important generalizations came to light among which special mention should be made of (i) the frequent correlation between caecal specialization and conditions elsewhere in the gut, and (ii) the fundamental pattern of the mesenteric connections and their associated blood-vessels. We convinced ourselves that diet had essentially no bearing on caecal morphology within the Primate order, and support for this was adduced from other mammalian orders. We also concluded that the form of the Primate caecum was linked with morphological features in other parts of the anatomy both in the alimentary and other systems and was thus dependent on phylogeny rather than environmental conditioning. So much obscurity has surrounded these points that we feel they need emphasis in this introduction.

The present investigation was undertaken in order to extend the above methods and principles beyond the Primates. The monotremes and marsupials were chosen

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for several reasons. Both orders differ widely in their anatomy from all eutherian mammals, each forming a distinct subclass. At the same time, however, evolutionary radiation has occurred in the members of both these groups resulting, especially among the Marsupialia, in convergent adaptations to the varying environmental conditions to which they have been subjected since the cretaceous period. Thus we find ant-eaters among monotremes, marsupials and eutherians. Vegetable feeders, honey-eaters and carnivores have evolved equally among the marsupials and the eutherians, besides many other parallel anatomico-physiological modifications. It is therefore of considerable interest to make comparison between the eutherian and the non-eutherian orders in respect of their alimentary anatomy and physiology. The non-eutherians in general would seem to be most suitable for testing some or all of our hypotheses.

Little detailed work has hitherto been carried out on the alimentary modifications of the monotremes and marsupials. It is true that Everard Home (1802 a, b, 1808) and Meckel (1826) gave excellent general accounts of the alimentary canal of the Platypus (*Ornithorhynchus*), the Echidna (*Tachyglossus*) and the Wombat (*Vombatus*), including figures of the caecum; but this pioneer work has not been followed up in detail. Owen (1841) made use of presence or absence of caecum in his attempt to classify the Marsupialia. More recent work by Mitchell (1905, 1916) and Mackenzie (various papers published between 1916–1918) was directed mainly to description of the external and internal appearances of the caecum without reference to its relations, peritoneal or otherwise. An exception must, however, be made in the case of Lönnberg's (1902 b) valuable contribution on the Koala (*Phascolarctos*) and several other marsupials. This work has been too lightly dismissed by later workers, with the result that the Koala has suffered the same kind of misrepresentation regarding its alimentary arrangements as the Rabbit (*Oryctolagus*). Both are, in fact, highly specialized animals, particularly in their digestive organs, both anatomically and physiologically. We shall return to this subject later, but meanwhile it should be noted that Mackenzie (1917) with some justification regarded the Koala as an extreme example of the correlation of a huge caecum with specialized vegetarianism.

Absence of caecum occurs among marsupials and eutherians and is evidently due to phylogenetic loss, for there is no evidence that the condition is a primitive mammalian feature, and much to indicate that a caecum of some kind is a heritage from reptilian ancestors. Reasons for phylogenetic disappearance are difficult to assess, though disuse atrophy is the most likely explanation, e.g. in the rigidly carnivorous Dasyuridae and the insectivorous *Notoryctes*, both of which exhibit gut-patterns morphologically similar to those met with in their respective eutherian counterparts. Once lost, a caecum cannot apparently be regained even with change from carnivorous to vegetarian habits. Therein a species betrays in its alimentary morphology its taxonomic relations rather than its environmental conditioning.

Carnivorous or insectivorous habits are not the only reasons for loss of the caecum, for among the marsupials we find the organ also lacking in *Dromiciops*, which is probably omnivorous, and in *Tarsipes*, a specialized honey-feeder. It will be recalled that we pointed out, in our previous contribution (1948), that in the

Giant Panda (*Ailuropoda melanoleuca*) the caecum is lacking. In this feature it agrees with other members of the taxonomic group to which it pertains, yet it is a specialized vegetable feeder normally as much limited dietetically as is the Koala (*Phascolarctos*). Yet the latter anatomically contrasts strongly in its possession of an enormous caecum. Mere vegetarianism, therefore, cannot be the sole factor in the evolution of a large caecum, though there may be some special property in the restricted range of leaves and shoots (in the instance of the Koala) that has a bearing on the caecal proportions.

Owen (1868) propounded the view that complexity of caecum was in inverse ratio to that of the stomach. This is frankly the case in ungulates, but Owen quoted also the Koala as an example. By analogy with the ungulates, it is feasible that the large caecum of the Koala is necessary as a site for bacterial digestion of cellulose or for the synthesis of essential vitamins, but it is clear, from what has been said, that the mere vegetarianism as such is not the only factor involved in the caecal hypertrophy.

In Primates we found that caecal complexity often occurred *pari passu*, with complexity elsewhere in the colon (e.g. in the Indriidae), and there are among the marsupials suggestive examples pointing to the same conclusion. There are likewise examples here of gastric complexity recalling that of the Primate family Colobidae, notably among the Macropodidae, but the caecum is never so reduced in these as in the Colobidae.

In one respect our task has been simpler than in dealing with the Primates, for the controversial matter of an *appendix caecalis* scarcely arises. Apart from the peculiar reduced vermiform caeca of the monotremes, the only non-eutherian genus in which the presence of a processus vermiformis has ever been postulated is *Vombatus*. This is dealt with fully, however, in its place hereafter and needs no further discussion at this stage.

Subclass PROTOTHERIA.

Order MONOTREMATIA.

Family I. ORNITHORHYNCHIDAE.

1. *Ornithorhynchus anatinus* Shaw. (Pl. 1, fig. 1.)

Has the small and large intestines forming a continuous passage of more or less uniform calibre throughout, except that the duodenum and rectum incline to be of greater circumference than the intermediate tract. Mitchell (1905, 1916) has adequately described the general gut-pattern and its mesenteries. There is a median point of fixation on the hind gut where it crosses the spine from right to left. On both oral and aboral sides of this fixed region the gut is provided with ample mesenteries carrying blood-vessels and lymphatics.

The caecum, as known since the observations of Home (1802 a) and Meckel (1826), is a small, vermiform outgrowth, some 17.5 mm. in length and of even calibre throughout, except that the apex inclines to become slightly bulbous. It is located on the antimesenteric border of the gut some 50 mm. to the oral side of the

level where the hind gut crosses the caudal transverse portion of the duodenum. It is provided with a short, thick mesotyphlon connecting its morphologically cranial border with the antimesenteric border of the terminal ileum. The ileal border of this fold is short, and the caecal and free borders about equal in length and twice that of the ileal border. The fold does not reach the tip of the caecum. The caecum receives its blood supply from a small artery which crosses the ventral aspect of the ileo-colic junction (i.e. morphologically dextral) and enters the mesotyphlon before giving terminal visceral branches. This vessel is a direct continuation of one of the main branches of the anterior mesenteric artery, which fan out in the right mesentery. Most of these branches are unconnected by loops (cf. *Echidna*), but a loop exists between two neighbouring stems that supply the right part of the colon. This is evidently the region figured by Mitchell as receiving a separate vessel and regarded by him as the homologue of the *ansa coli dextra*. Numerous minute lymphatic glands accompany the principal mesenteric vessels, and are even more numerous as these divide as they approach the gut. There are no special lymphoid developments in the ileo-colic region.

Family II. TACHYGLOSSIDAE.

1. *Tachyglossus aculeatus* Shaw. (Pl. 1, fig. 2.)

Two examples of the Common *Echidna* have been examined, one from Australia and one presumed from its size to be of Tasmanian origin (*T. a. setosus* Geoffr.).

In both animals the gut-pattern much resembles that of *Ornithorhynchus*—as found by Mitchell and by Mackenzie (1918), but the calibre is relatively and absolutely greater throughout. The rectum tends to assume a bloated fusiform contour. There is the usual primitive dorsal point of fixation of the hind-gut, to the right and left of which point the gut is supported by ample mesenteries. The right mesentery supports the small intestine and proximal part of the colon, and contains a liberal vascular tree which is looped throughout. A branch from one of these loops proceeds towards the region of the ileo-colic junction, where it divides to embrace the intestine. The dorsal (i.e. sinistral) vessel alone proceeds subserously on to the caecum—the opposite of the condition in *Ornithorhynchus*. The vessel finishes its course in the mesotyphlon. Lymphatic glands are distributed as in *Ornithorhynchus*, but are relatively larger and less numerous.

The caecum has the same vermiform character as in *Ornithorhynchus*, but is individually variable in its details, as found by Mackenzie. The caecum is 16·8 mm. long in the Tasmanian example and 13 mm. in the Australian. In the Tasmanian specimen it depends freely from the antimesenteric border of the gut, with a thick short mesotyphlon connecting its cranial border with the antimesenteric border of the terminal ileum. The mesotyphlon does not pass to the end of the caecum. In the other, the proximal part of the blind gut is held firmly against the ileum by virtue of the shortness of the mesotyphlon, leaving the distal 9·2 mm. bent back on itself in the direction of the colon. In the Tasmanian example the distal part of the caecum is bulbous, as in *Ornithorhynchus*, but in the Australian specimen the

blind end is conical. According to Mackenzie the caecum of *Tachyglossus* is very variable as regards its lumen, this being sometimes absent. In our Tasmanian example it is certainly present and shows no evidence of degeneration.

2. *Zaglossus bruijnii* (Peters & Doria). (Pl. 1, fig. 3.)

In an adult male preserved in the Royal College of Surgeons we found the alimentary tract had been detached from its connections, but in places, sufficient of the mesentery had been left attached to the gut for us to make some observations on the vessels. This was fortunately the case at the ileo-colic junction, where it was possible for us to make an injection into the local branches of the anterior mesenteric artery.

The general gut-pattern was apparently in much the same condition as in *Tachyglossus*, but there was presumably a relatively shorter hind-gut, possibly lacking the left colic loop so well shown by *Tachyglossus*. The calibre of the gut appears to be rather large in both small and large intestine; when distended artificially the diameter attains 25.7 mm. If anything, there is a slightly less calibre at the beginning of the colon than at the end of the ileum, though this may be purely a physiological phase and not permanent or constant. The rectum is not markedly dilated in comparison with the rest of the gut. The gut is smooth-walled throughout and unsacculated.

The caecum in *Zaglossus* is a flask-shaped diverticulum from the antimesenteric border of the gut. It is connected by a narrow neck, of external diameter 3.5 mm. The diverticulum gradually broadens to a maximum diameter of 8.4 mm., thereafter rapidly diminishing to form a rounded fundus. Its total length is 16.8 mm.—exactly the same as in *Tachyglossus aculeatus setosus* of similar body-size.

Externally the caecum is smooth, but marked by a number of transverse creases, especially near the neck. There is no mesotyphlon, but a longitudinal thickening of the serous and longitudinal muscular coat along the ileal aspect of the viscus seems to represent a vestige of this structure. No vessels are located in this thickening. The blood supply of the caecum is derived from one of the transverse arteries supplied to the gut from the termination of the anterior mesenteric. These transverse vessels lie more deeply than usual, amongst the muscular fibres of the gut-wall rather than subserously, and in the preserved material can only be made out after injection and observation by transillumination. The vessel to the caecum is morphologically dextral in position as in *Ornithorhynchus* and is continued from an artery supplying the proximal colon. A similar vessel is found on the sinistral side of the colon, but does not appear to be continued on to the caecum. The caecal artery sweeps orally in a gentle curve so as to gain the caecum on the ileal aspect of its constricted neck, and gives small oblique branches to the colon *en route*. Numerous small lymph-nodes lie along the mesenteric border of the gut as in the other Monotremata, whilst large numbers of still smaller nodes are scattered through the mesentery.

The wall of the caecum is relatively thick but the lumen is large, communicating however with the general lumen of the intestine by a very constricted opening. It is difficult in the material at hand to inflate the caecum *via* the gut without

exercising considerable pressure. In sections lymphoid tissue is present in small, thin plaques at local sites in the submucosa. The microscopic appearances thus differ considerably from those of the vermiform tip of the caecum in the *Lagomorpha* (*Lepus*, *Oryctolagus* and *Ochotona*) where immense masses of lymphoid tissue occur throughout.

Subclass METATHERIA.

Order MARSUPIALIA.

Suborder POLYPROTODONTIA.

Superfamily DIDELPHOIDEA.

Family I. DIDELPHIDAE.

1. *Didelphis marsupialis* Linn. Common American Opossum. (Pl. 1, fig. 4.)

Two adults, a male and a female, of *Didelphis marsupialis virginiana* have been examined, also an advanced pouch-foetus of *D. m. karkinophaga*.

In this species the large intestine is short and wide, the ileo-colic junction being located a little to the right of the median plane in close proximity to the primitively fixed segment of the colon, where the spine is crossed transversely.

The caecum is a long, capacious, blind sac extending first to the right and then caudalwards from the ileo-colic junction, occupying the right flank (Pl. 1, fig. 4). In an adult male of 393 mm. body length it measures 77 mm. long and has a diameter of 30 mm. Its wall is smooth and its apex blunt and rounded. The lumen is constricted at the caeco-colic junction. The general axis of the caecum is continuous with that of the proximal colon, into which the ileum opens from behind forwards.

There is, connecting the left wall of the caecum with the terminal ileum, an extensive triangular median mesotyphlon whose borders measure in the adult male: ileal border 16 mm.; caecal border 35 mm., and free border 35 mm. This membrane carries vessels derived from a smaller fatty fold which crosses the ileo-colic junction sinistrally. The main vessel enters the mesotyphlon in the acute ileo-caecal angle and crosses distally parallel with and a short distance from the concave left border of the caecum, supplying branches thereto as well as three recurrent branches to the antimesenteric border of the ileum. A dextral fatty fold crosses the ventral aspect of the ileo-colic junction, transversely to the axis of the ileum. It carries a small artery to the basal part of the ventral wall of the caecum; this communicates with the proximal transverse branch of the principal caecal artery. No lymphatic glands could be detected in either dextral or sinistral plicae.

Mitchell figures the principal caecal vein as double over the distal part of its course, thereafter running singly and independently to embouch into the cranial end of the anterior mesenteric vein.

No essential differences are notable in the pouch-foetus of *D. m. karkinophaga*, except that the dextral vascular fold forms a raised membrane, with underlying peritoneal recess (ileo-colic fossa).

2. *Didelphis paraguayensis* Oken. Azara's Opossum. (Pl. 2, fig. 5.)

The disposition of the large intestine in Azara's Opossum is very similar to that of the Virginian Opossum, but it is relatively considerably larger, due to the elongation of its aboral portion which is produced into a distinct ansa quite unrepresented in *D. marsupialis*. The ileo-colic junction is in the same position as in the latter species, but the caecum is relatively longer and narrower. In an adult male of body length 285 mm. the caecum has a straight length of 63 mm., i.e. a ratio of $1/4.5$ compared with $1/5$ in *D. marsupialis*. The proximal third of the blind gut was contracted in the adult male, whilst the rest was dilated and had a diameter of only 13 mm. compared with 30 mm. in the larger species. The caecum has the same general form, unsacculated and blunt-ended as in *D. marsupialis*. The peritoneal relations are also similar, but the mesotyphlon is relatively more extensive, proceeding farther toward the caecal apex. Its borders have the following dimensions: ileal 20 mm.; caecal 40 mm.; free 27 mm. Vascular folds and course of blood-vessels are as in *D. marsupialis*, but no communication could be traced between the dextral artery and the proximal transverse branch of the main sinistral vessel.

3. *Marmosa mitis* Bangs. Bang's Opossum.

This is one of the larger species of *Marmosa*. In an adult female with vertex-rump length 122.5 mm. we find the caecum to be 18 mm. long. In disposition of the parts of the hind-gut it agrees well with *Didelphis marsupialis*, the ileo-colic junction being placed well forwards in the right flank and the caecum proceeding caudalwards therefrom without change of calibre. The blind-gut is a simple tubular structure with rounded apex. Its mesotyphla are as in *Didelphis*, the sinistral fold and its contained vessel being strongly developed, and a peritoneal pocket found between it and the median fold.

4. *Marmosa* ? sp. Murine Opossum.

In an example of one of the tiny species of *Marmosa* we find the morphology as in *M. mitis*, but the proportions are quite different. In our specimen with vertex-rump length 45.8 mm. the caecum measures 12 mm.

5. *Metachirus opossum* (L.). Quica Opossum. (Pl. 2, fig. 6.)

This species was briefly reported upon by Sonntag (1921) who found a capacious caecum two and a half inches long, the interior of which was devoid of septa and folds. Its mesotyphlon had a concave free edge and was "bisected by an artery"

In a female adult we found the large intestine very similar to that of *Didelphis marsupialis virginiana*, but if anything still shorter proportionally, since its right portion was almost absent, the ileo-colic junction being high up against the liver only slightly to the right of the median plane. The sac-like caecum is of the same calibre as the colon and continues in line therewith, first to the right, then curving caudad in the dorsal part of the right flank to end in a blunt, rounded apex which shows no terminal narrowing. The blind-gut in this animal measured 33 mm. long. The caecum is tethered by a median mesotyphlon flanked by both

dorsal and ventral vascular folds. The principal caecal artery, however, was carried in the ventral fold, which delivered it to the median fold wherein a recurrent ileal branch was conveyed. The artery did not "bisect" the mesotyphlon, but kept close to the caecal wall.

In a second adult female the arrangements were almost identical with the above, save that the caecum, measured fresh, was 36 mm. long. The vascular injection on this specimen was so satisfactory that a more detailed picture was obtained. The principal vessels were exactly as in the previous specimen, the dextral vessel being the larger and supplying a greater extent of the caecal wall. After crossing the ileo-colic junction obliquely, this vessel divides into a smaller medial and larger lateral division. The medial artery courses along the mesenteric border of the caecum towards its apex, giving off two recurrent ileal vessels, one along the antimesenteric border of the ileum, the other in the free border of the mesotyphlon. They form an anastomotic circle by their fusion on the ileal wall. The large ventral division of the dextral caecal artery gives a transverse branch, soon after its origin, continuing thence obliquely over the ventral wall of the gut, forming a looped anastomosis with the medial division and also with branches of the sinistral artery.

The sinistral caecal artery arises some distance proximal to the ileo-colic angle from the terminal portion of the anterior mesenteric. Proceeding across the ileo-colic junction, it gives a transverse twig to the adjacent wall of the large gut, then a small twig to the ileo-caecal angle, where it forms a looped anastomosis with the medial longitudinal division of the dextral artery, continuing thereafter towards the apex caeci more or less parallel to the last-mentioned vessel (*vide* Pl. 2, fig. 6).

6. *Monodelphis brevicaudata* (Erxleben). Red-flanked Opossum.

In an adult male of this Guianan species, the arrangements are similar to the above, but the caecum is relatively shorter and more rounded. Both genera lack the terminal constriction met with in *Didelphis*.

7. *Lutreolina crassicaudata* (Desmarest). Thick-tailed Opossum. (Pl. 2, fig. 7.)

A further degenerative change is met with in the caecum of this large opossum, for the organ measures but 17.8 mm. long. It forms a relatively straight blind tube projecting to the right from the antimesenteric border of the gut opposite the ileo-colic junction. The latter lies against the visceral aspect of the right liver lobe and shows no appreciable change of calibre in passing from ileum to colon. The ileum sweeps craniad to gain the junction.

The caecum is more constricted at its base than towards the apex. It is connected by a triangular mesotyphlon with the antimesenteric border of the ileum, and supplied by a sinistral vessel that gains the caecum in a vascular fold dorsally. It proceeds thence into the mesotyphlon, which it bisects, giving two branches to the ileum and two to the caecum. A minute dextral vessel terminates on the proximal colon without gaining the caecum.

In a second example examined in the fresh state and again after arterial injection the above details were confirmed. The caecum in this specimen, an adult male, measured 23 mm. in length, the excess over the previous specimen being due to the elongation of the constricted basal segment. The arrangement of the vessels in this example is illustrated in Pl. 2, fig. 7.

8. *Chironectes minimus* (Zimmermann). Water Opossum.

The only specimen suitable for the study of the caecal region was an advanced pouch-foetus of 78 mm. length from vertex to rump. Unfortunately the viscera had been disturbed and partially damaged, but as far as could be ascertained the gut-pattern and morphology of the ileo-caecal region appear to be very primitive, quite different from the other Didelphidae (with the exception of *Dromiciops*, which probably represents the final degenerative stage). The nearest equivalent is met with in the *Caenolestidae* discussed below.

The colo-rectum is a short, wide passage confined to the dorsal region of the abdomen, and taking a straight course from the ileo-colic junction to the anus, as in *Caenolestes*. This part of the gut is broad in calibre at its oral end, narrowing gradually aborally. The ileum opens on the right side of the vault of this rather elongated, pyriform sac, and the caecum is a short, sausage-shaped diverticulum 4.5 mm. long, springing also from the right side, a little caudad from the ileal entrance. The outgrowth is directed aborally, being curved over to the right and its apex pointing caudally, the reverse of the condition in *Caenolestes*. The condition of the specimen precluded satisfactory observations on the peritoneal relations and vacular supply, but obviously from the morphological standpoint these should prove of exceptional interest.

9. *Dromiciops australis* (Phillipi). Chiloe Island Opossum.

So far as we are aware, the internal anatomy of this peculiar insular opossum has not hitherto been described. From the present point of view the most remarkable feature is the complete absence of caecum. The gut-pattern is very primitive and falls into line with that of the carnivorous *Dasyuridae*.

Large and small intestine are not differentiated from each other, agreeing in calibre and all outward features. There is the usual short area of fixation where the gut crosses the median line before its final straight portion leading to the anus. The anterior mesenteric vessels supply all the coils to the right of this fixed area, whilst the posterior mesenteric artery supplies the region from the fixed point onwards. The peritoneal band which binds the fixed area to the last portion of the duodenum extends for 5 mm. along the straight part of the gut. It is separated by a pocket—open caudalwards—from the underlying parietal peritoneum.

These findings have been confirmed on a second specimen.

Superfamily DASYUROIDEA.

Family I. DASYURIDAE.

The carnivorous marsupials forming the family Dasyuridae are all in agreement in possessing a simple, relatively short gut without trace of caecum. The following material has been examined to confirm this statement:—

1. <i>Thylacinus cynocephalus</i> (Harris), 1808	1 adult
2. <i>Sarcophilus harrisi</i> (Boitard), 1841	2 adults
3. <i>Dasyurus quoll</i> (Linn.), 1777	1 adult
4. <i>D. maculatus</i> (Kerr), 1792	2 pouch-embryos
5. <i>Dasyuroides byrnei</i> (Spencer), 1896	1 adult
6. <i>Phascogale tapoatafa</i> (Meyer), 1793	1 adult
7. <i>P. macdonnellensis</i> (Spencer), 1895	1 adult
8. <i>Sminthopsis crassicaudata</i> (Gould), 1844	1 adult
9. <i>S. murina</i> (Waterhouse), 1838	1 adult
10. <i>Antechinus flavipes</i> (Waterhouse), 1838	2 adults
11. <i>Myrmecobius fasciatus</i> (Waterhouse), 1836	1 adult and 2 pouch-embryos

The intestine and mesenteries of *Myrmecobius* are figured in Pl. 2, fig. 8 as illustrative of the family. The capacious duodenum of *Thylacinus* is noteworthy, whilst in *Sarcophilus* the arrangement of the arterial loops and the extent of the broad, anangious peritoneal fold connecting the duodenal mesentery with the root of the mesocolon (ligamentum colico-duodenale of Krause, Klaatsch, Beddard, 1908) are characteristic features. This fold is likewise highly developed in *Myrmecobius*.

In *Dasy cercus*, regarded by Wood Jones as perhaps the most generalized member of the family, this author found (1949) after a wide-bored duodenum a very simple intestine without definite caecum, but in some specimens a change of calibre and in character of contents "would almost seem to mark the site of a physiological change in intestinal function".

Family II. NOTORYCTIDAE.

The Marsupial Mole (*Notoryctes typhlops*) agrees with the Dasyuridae in the absence of caecum and the simple gut pattern. This has been confirmed by personal observation on four specimens. The gut has been figured by Mitchell (1916).

Superfamily CAENOLESTOIDEA.

Family CAENOLESTIDAE.

1. *Caenolestes fuliginosus* (Tomes), 1863. (Pl. 2, fig. 9.)

This curious and primitive marsupial has been the subject of monographic study by Osgood (1921) who described and figured a small caecum at the junction of small and large intestine, but without giving details or reference to vascular supply.

Two adult examples, a male and a female, have been examined with the following results.

The caecum is a short, sausage-shaped diverticulum which springs from the antimesenteric border of the intestine only a short distance proximal to the rectum.

There is no change of calibre demarcating small from large intestine, but the caecal diverticulum has about half the calibre of the intestine. The direction of the caecal axis is cranialwards and slightly to the left, the apex lying adjacent to the lower pole of the left kidney. From base to apex it measures in the female 4.2 mm. long, that of the male being somewhat shorter. Osgood also noticed an individual variation in length, 4.5 mm. in one and 5.4 mm. in another. There is a well-defined lumen and the wall, when stretched, exhibits a reticulate appearance, due to the relatively darker appearance of the narrow tracts separating paler ovoid areas—presumably composed of lymphoid tissue.

The caecum is—contrary to Sonntag's (1921) inference from Osgood's description—moored in position by two peritoneal folds or mesotyphla, a morphologically median fold and a shorter dextral fold. The former is anangious, the dextral fold carrying vessels to the base of the caecum and neighbouring part of the intestine. Both folds have free falciform margins directed cranially. The median fold connects the median line of the antimesenteric border of the terminal ileum with the whole length of the adjacent border of the caecum. The dextral fold springs from the right leaflet of the common intestinal mesentery and proceeds across the surface of the ileo-colic junction towards the right surface of the base of the caecum, where it terminates.

The ileo-colic opening is a simple, small, circular orifice, without adjacent modification of the intestinal mucosa. It is situated at the line of demarcation between the relatively thin-walled ileum with its villous mucous membrane and the thicker-walled colo-rectum whose mucous membrane is smooth, and raised into longitudinal folds. There are no taeniae coli or sacculations.

2. *Orolestes inca* Thomas.

In an adult male of this species examined at the British Museum (Nat. Hist.) the caecum is similar in position, shape and general form to that of *Caenolestes*, but is relatively shorter and broader, measuring 2.3 mm. long. The peritoneal folds are quite vestigial here, but the vessels are as in *Caenolestes*.

Superfamily PERAMELOIDEA.

Family PERAMELIDAE.

1. *Isoodon obesulus* (Shaw). Short-nosed Bandicoot. (Pl. 3, fig. 10.)

The arrangement of the gut recalls that of *Didelphis*. There is a simple arched colon, with short or absent right limb, transverse portion of broad calibre passing without definitive splenic flexure into a narrower left limb. The ileo-colic junction is very oblique and placed well forwards on the right side. The capacious, incipiently sacculated caecum springs from the right aspect of the gut and proceeds caudally in the right flank, terminating in a roundedly conical upturned apex. An extensive median mesotyphlon connects the last inch or more of the ileum with the medial border of the caecum—extending to the apex thereof. It carries some recurrent vessels towards the ileum. The blood-supply of the caecum is carried in a well-marked dextral fold, which forms the ventral wall of a deep fossa as shown in

the figure. A similar fold is raised by the first artery supplying the colon, but here the free edge is directed cranially instead of caudally. Between the two vascular folds the intestine is supplied by a leash of small vessels passing directly to the gut; these are responsible for the vascularization of the ileo-colic junction and basal portion of the caecum. There is no sinistral fold or vessel.

This species has been briefly referred to by Sonntag (1921) who found the caecum as in *Macrotis* (reported on by Mitchell, *vide infra*) and possessing a mesotyphlon, whereas *Macrotis* lacks this membrane.

2. *Perameles nasuta* E. Geoffr. Long-nosed Bandicoot. (Pl. 3, fig. 11.)

The large intestine agrees with that of *Isoodon*, but its right extremity is more convex, the ileum entering the caeco-colic junction at a right angle. The caecum is smooth and unsacculated, relatively longer than in *Isoodon*, in line with and having the same calibre as the colon. It describes a gentle curve, convex to the right and ends in a broadly conical extremity.

A median mesotyphlon, short at its ileal attachment, but extending almost to the apex of the caecum, is found in the ileo-caecal angle. It is quite avascular. The caecal vessels are transmitted in a short, thick dextral fold. There is a low, fusiform, fatty fold sinistrally at the ileo-colic junction, but this carries no appreciable vessels. The general arrangement therefore agrees with that of *Isoodon* and of the *Perameles* (species unstated) described by Mackenzie.

3. *Macrotis lagotis* (Reid) (olim *Peragale lagotis*). Rabbit Bandicoot. (Pl. 3, fig. 12.)

Mitchell (1905) briefly described the gut of this species stating that it differed from that of *Perameles* and *Isoodon* in possessing a short, wide caecum passing, without change of calibre, into the colon. He made no reference to peritoneal relations or vessels. Sonntag (1921 b) says that there is no mesotyphlon.

In an adult female from Charlotte Waters, Central Australia, we find a capacious caecum, continuous, without change of calibre into the colon, as described by Mitchell. But we cannot agree that it is relatively shorter than in *Perameles*, nor indeed anything like the representation of it in Mitchell's figure.

We find the ileo-colic junction placed well forwards against the right lobe of the liver, the ileum terminating in a forward direction. From here there is a well-marked transverse colon, supported by a distinct but short mesocolon. An incipient left colic loop (splenic flexure) is developed on the left. The caecum occupies the right flank and is much folded upon itself. It retains its broad calibre throughout, ending in a rounded apex.

The intermediate mesotyphlon is short and appears to be anangious. There is only one caecal artery, the dextral, which sweeps across the ventral aspect of the terminal ileum in a broad peritoneal fold which masks the last portion of the ileum completely. A deep fossa exists between this fold and the true mesotyphlon. After gaining the caecal wall—about a third the way along the blind-gut—the

vessel runs the remainder of its course subserously. No dorsal (sinistral) branch could be detected, nor any corresponding peritoneal fold, but the material was not by any means favourable.

4. *Echymipera aruensis* (Peters & Doria). Aru Island Bandicoot. (Pl. 3, fig. 13.)

This small New Guinea Bandicoot has a more primitive gut than any of the continental forms. It recalls that of *Chironectes* and *Caenolestes*, for the ileo-colic junction is situated at the oral end of a relatively simple, dorsal, more or less median large intestine, which is only slightly bowed to the left. The terminal ileum arches over from right to left immediately caudad of the liver.

The caecum is a short, wide, flask-shaped sac, wider at its fundus than its attached end. It springs from the convex, antimesenteric border of the intestine and is directed cranially. It measures 15.5 mm. long in an adult female of 122 mm. vertex-rump length. There is a simple, but extensive mesotyphlon connecting the antimesenteric wall of the terminal ileum with the whole length of the adjacent wall of the caecum. It carries no vessels. The caecum is supplied by equal-sized sinistral and dextral arteries which run in low peritoneal folds across the ileo-caecal angle—a very generalized arrangement.

Suborder *DIPROTODONTIA*.

Superfamily PHASCOLOMYOIDEA Pocock.

Family I. VOMBATIDAE.

1. *Vombatus mitchelli* (Owen, 1830). Common Wombat. (Pl. 4, fig. 14.)

As in all diprotodont marsupials, the large intestine of the wombat is greatly elongated. From a fixed dorsal locus in the median plane, the hind-gut extends freely to left and right in numerous coils supported in corresponding left and right mesocolons.

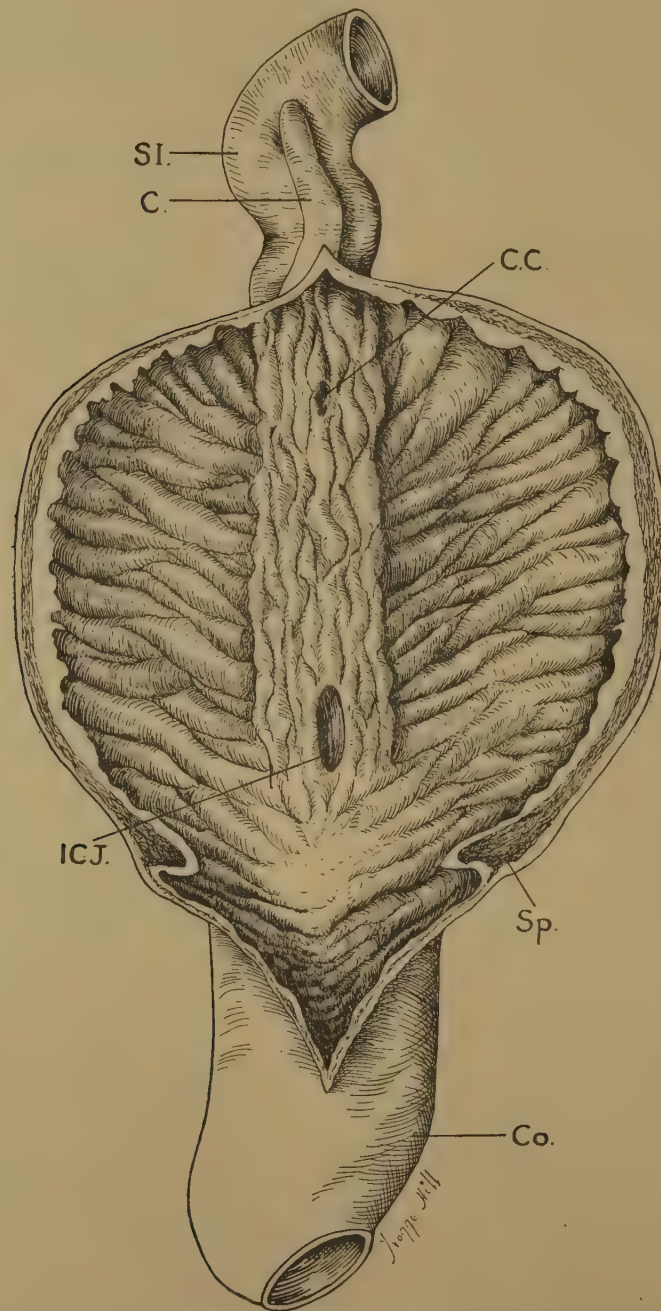
The elongation of the right or oral segment of the colon is so great as to have rotated, in a clockwise direction, the caput caecum coli far beyond the usual position in the right flank or right iliac fossa towards a more central and cranial position just caudal to the fixed median segment of the colon. In some specimens it is possible to detect incipient sacculation of the colon on its antimesocolic wall; but there are no taeniae.

As noted by Mackenzie, the ileo-caecal region is relatively fixed, being adjacent to the root of the mesentery, which is here shortened. The ileo-colic junction is approximately right-angular. The proximal part of the colon is dilated to form an expanded sac, projecting as a convexity from the antimesenteric border. This has been identified as caecum almost universally by anatomists (Home, 1808; Knox, 1826; Flower, 1872; Mitchell, 1905; Beddard, 1908; Mackenzie, 1918 a) though Lönnberg (1902) did not consider this interpretation to be correct.

From a site in the angle between the above-mentioned sac and the antimesenteric border of the terminal ileum there springs a vermiform structure recalling the caecum of the Monotremata. This varies somewhat in length, Mackenzie giving the average as 4.5 cm., and normally it presents a narrow lumen. It is by all anatomists

except Lönnberg considered to be homologous with the vermiform appendix of the Hominoidea. Mackenzie has discussed Lönnberg's views and considers his arguments invalid. Mitchell took a more lenient view of them. It will be necessary to go into the question again after certain new observations have been recorded here.

Fig. 1.



Vombatus mitchelli. Interior of caecum and commencement of colon.
 C., caecum ; C.C., caeco-colic valve ; Co., colon ; ICJ., ileo-colic junction ;
 SI., small intestine ; Sp., sphincter muscle.

In the first place, the vermiform structure is an outgrowth from the medial wall of the basal colic sac, its point of attachment being immediately beneath the ileo-colic angle. The tube is closely adherent to the ileum for some distance, thereafter becoming more free, but connected to the ileum by a short, thick median mesotyphlon. This, however, is not carried to the apex of the blind sac, the terminal third or more of which is quite free. The manner of embouchment of ileum and vermiform process into the colon has been fully described in the accounts of Owen, Flower, Lönnberg and Mitchell, and has in most essentials been confirmed by us; but it is evidently subject to some individual variation. Both Flower and Mitchell figure the vermiform process and ileum as opening by separate orifices upon a common raised eminence telescoped into the basal colic sac, such that, as Mitchell remarks, "it is impossible to regard the so-called vermiform appendage as a continuation of the globular proximal end of the colon". In one of our examples the telescoping of the ileo-caecal eminence with the proximal colic sac is extreme, the intramural part of the lumen of the vermiform process being at least a third the total length thereof. Moreover, a fleshy, oedematous fold of mucosa separates the two openings on the summit of the eminence. In the other example the two openings are farther apart, on a longitudinal raised ridge whose mucous membrane presents undulating longitudinal folds, in marked contrast to the more transversely folded mucosa of the neighbouring colic wall. A sphincter muscle is located on the colic wall immediately to the aboral side of the proximal colic sac (text-fig. 1).

The vascular supply of the ileo-caecal area seems to be of some value in determining the correctness or otherwise of Lönnberg's views.

The distal continuation of the anterior mesenteric artery is carried on to the dorsal (i.e. sinistral) aspect of the ileo-colic junction, which it crosses transversely to the axis of the ileum. Thence it proceeds subserously to the vermiform process, being continued to its tip. As it crosses the ileo-colic junction, the artery gives branches to right and left—a single one to the left, supplying the terminal ileum and four or five to the right, supplying the dorsal wall of the proximal colic sac. After gaining the vermiform process, a single branch is given to the left. This enters the mesotyphlon, as in *Perameles*, and supplies the antimesenteric wall of the terminal ileum.

On the ventral side no vessel is carried to the vermiform process. A small vessel passes on to the gut wall near the ileo-colic junction and gives a branch longitudinally to the terminal ileum. On the aboral side of this a small arterial arcade supplies vessels to the ventral wall of the proximal colic sac.

Mackenzie has endeavoured to combat Lönnberg's interpretation by postulating that the caput coli of *Vombatus* represents a final evolutionary step on Treve's (1885) well-known classification of types of caecum—represented at various ages in Man and the other Hominoidea. He would have us believe that, in *Vombatus*, the medial caecal sacculation has entirely degenerated, thus bringing the root of the appendix into contact with the antimesenteric wall of the ileum, as occasionally occurs in Man (Treves' fourth type).

Aside from Lönnberg's argument based on the manner of opening of the vermiform tube with the hind-gut proper, the vascular supply (including that of the

lymphatics so far as we were able to inject them on formalin-preserved material) seems to support his interpretation, viz. :—that the vermiform tube is morphologically a vestige of the whole caecum, whilst the so-called caecum—here referred to as proximal colic sac—is a secondarily developed dilatation. The arrangement is paralleled to some extent by conditions in the Hyracoidea, only there the secondary sac has developed to the ileal side of the true or morphological caecum, which is sometimes quite small, though always quite identifiable by its peritoneal and vascular relations. (The only correct interpretation ever given of the morphology of the various caecal structures of the Hyracoidea and referred to by numerous anatomists is that given by Kostanecki, 1922, with whose view we are in entire agreement (Rewell, 1949). We consider, therefore, the likeness between the ileo-caecal region of the Wombat with that of the Hominoidea to be quite superficial and regard Lönnberg's interpretation as correct—without prejudice to his speculations on the causal mechanism behind the morphological peculiarities.

Additional support to our view is given by the statement of Owen (1836) that the colon of the Wombat is so deeply indented that the sacculations produced next to the "caecum" (our proximal colic sac) may be very similar to it. His small figure certainly shows this. It is a very simple sketch, almost a diagram, but is best interpreted as showing a proximal colon with relative elongation of the morphologically ventral wall with several sacculations of which the "caecum" is only the first and largest. In an earlier paper (1841) he had considered the small structure to be a "vermiform process" and had placed its bearer in a separate group as the "Rhizophaga".

Superfamily PHALANGEROIDEA.

Family I. PHALANGERIDAE Thomas.

Subfamily TARSIPEDINAE.

1. *Tarsipes spencerae* Gray. Honey-Phalanger.

This highly specialized Phalanger differs from all the other members of the family, and indeed from all the diprotodonts, in lacking all trace of caecum (Tullberg, 1899; *vide* Lönnberg, 1902). This fact is no doubt correlated with the very restricted and specialized diet of honey upon which these animals exclusively subsist.

We have examined an adult female and an advanced pouch-young.

Subfamily PHALANGERINAE.

2. *Trichosurus vulpecula* (Kerr). Vulpine Phalanger or Silver-grey "Opossum". (Pl. 4, fig. 15.)

This commonest of all phalangers may be taken as typical of the family, and used as basis for comparison in dealing with other genera. The visceral anatomy of this species is well known from the writings of Martin (1836 a), Owen (1841), Oppel (1897 a, b), Lönnberg (1902), Mitchell (1905), Mackenzie (1918 a, 1918 b)

and Sonntag (1921), all of whose accounts are in substantial agreement. We ourselves have examined three adults and an advanced pouch-young.

We agree with Mitchell's assessment of the general arrangement and mode of fixation of the colon, with its short, relatively straight right limb, supported on a moderate mesocolon, in contrast with the much coiled aboral (left) limb.

The ileo-colic junction is rectangular and lies in the right flank. Extending caudally from the junction, in alignment with the proximal colon, is the long, greatly coiled caecum. This is cylindrical throughout most of its length, slightly wider in diameter than the colon, smooth-walled and ending distally in a pointed conical extremity, the tip tending to become vermiform and upturned.

This huge caecum is tethered by a considerable sheet of peritoneum which forms an adequate mesotyphlon, bearing quite large blood-vessels. It extends distally almost to the tip of the organ, having an elongated falciform free edge carrying the main caecal artery. Traced proximally this mesotyphlon is found to divide into two sheets, one containing fewer and smaller vessels appearing to come off the main sheet in a ventral direction to attach itself in the ileo-caecal angle and along the antimesenteric border of the terminal ileum. The other (dorsal) sheet, which appears topographically to be a continuation of the main sheet, may be traced cranially behind the terminal ileum for some 50 mm., finally ending in an oblique attachment to the dorsal (sinistral) aspect of the ileal mesentery. The principal caecal vessel continues in this dorsal sheet and becomes hidden by a chain of lymph-glands located over the site of union with the anterior mesenteric arterial stem. Between these two peritoneal folds or mesotyphla is a deep triangular pocket.

The attachment of the peritoneal folds, as well as the pattern of the associated vessels, determine their morphology. Clearly the primary mesotyphlon is comprised of (a) the ventral relatively avascular fold plus (b) the distal sheet beyond the union of (a) with the dorsal fold. The dorsal sheet is the sinistral or vascular mesotyphlon which, on account of the great development of the caecum and the necessarily large size of its vasculature, has annexed the distal part of the true or intermediate mesotyphlon as a pathway for distribution of the vessels to the viscus. In doing this the two developmental parts of the mesotyphlon have been pulled out of alignment by the elasticity of the wall of the main caecal artery.

On the ventral aspect of the ileo-colic junction is a small serous fold carrying an anastomotic vessel from the sinistral caecal artery around the dextral side of the gut, as shown in Pl. 4, fig. 15. Another larger vessel runs along the line of fusion of the dorsal and intermediate mesotyphlon, whilst in the free edge of the ventral wall of the pocket is a recurrent artery which supplies terminal ileum and ileo-caecal angle, as well as the basal part of the ventral wall of the caecum.

3. *Phalanger orientalis* (Pallas). Cave Phalanger or Grey Cuscus.

Two adult specimens of this Cuscus have been examined, a male and a female. In both the disposition of the large intestine, including the caecum and its peritoneal and vascular relations, is exactly as in *Trichosurus*, apart from minor variations in detail.

The large intestine and caecum are very capacious, but unsacculated. In diameter they measure in the male 40 mm. and in the female 25 mm. The caecum terminates in a distinct vermiform upturned tip which measures 30 mm. long in the male and 20 mm. in the female.

The dorsal peritoneal sheet proceeds cranialwards for some 60 mm. before finally uniting with the dorsal (sinistral) leaflet of the mesenterium commune. At the point of fusion its free edge contains a large lymph-gland associated with the stem of the main caecal artery. The vascular arrangements are precisely as in *Trichosurus*.

4. *Acrobates pygmaeus* (Shaw). Pygmy Flying-Phalanger.

Of this species we have examined only a small pouch-foetus of 31.7 mm. crown-rump length (fixed in extended position) (*vide* Hill 1951).

Here the large intestine is less advanced in development than in the material of adult *Trichosurus* and *Phalanger* described above, the ileo-colic junction being placed anteriorly against the visceral aspect of the right lobe of the liver, as, for example, in advanced foetal and neonatal Primates. This is not the case, however, in pouch-foetuses of *Trichosurus* of less advanced development than this *Acrobates*. In the *Trichosurus* the caecum has already attained its adult relations and proportionate development to the rest of the gut. From this anterior position in *Acrobates* the caecum projects to the right, curving thence caudalwards. It measures 5 mm. long and is, compared with the rest of the gut, thick-walled. It gradually diminishes in calibre distally towards its tip. There is a sudden transition at the caeco-colic junction, with all the appearances of a sphincter mechanism. The colon is much wider in calibre than the caecum. The ileum joins the latter by a right-angled union. The peritoneal relations are as in *Trichosurus* and *Phalanger*.

5. *Cercaërtus nana* (Desmarest) (olim *Dromicia nana*). Common Dormouse Phalanger. (Pl. 4, fig. 16.)

A single specimen of this marsupial, an adult female, was available.

Its gut-pattern is closely similar to that of the *Acrobates* pouch-foetus just described, and recalls, in its details, the arrangement in *Tarsius* among the Primates (*vide* Hill & Rewell, 1948). The large intestine forms a simple arch, with very short transverse portion, which is tethered down on the ventral aspect of the duodenal area. The ileo-colic junction is situated, in contact with the posterior aspect of the large liver, a little to the right of the median plane. The terminal ileum approaches the junction from behind forwards, forming a more or less right-angled junction, but showing some constriction at the site of the union.

From the ileo-colic junction the sausage-shaped, smooth-walled caecum proceeds to the right, afterwards curving backwards in the dorsal part of the right flank. Its tip was upturned to the right in our specimen. The apex caeci is rounded and shows no terminal contracted region. The general calibre is the same as that of the colon, or slightly greater. Its total length is 13.5 mm.

Cercaërtus is also exceptional among the phalangiers—so far discussed—in respect of the caecal peritoneal appendages and their associated vessels, agreeing, however, with *Dactylopsila melampus* considered below. Dextral and intermediate mesotyphla are alone represented; they are quite independent throughout and the only caecal artery is the one carried in the dextral fold, which is the larger of the two peritoneal sheets.

6. *Eudromicia caudata* (Milne-Edwards). Long-tailed Dormouse-Phalanger.

In an adult female specimen from N.E. Guinea, measuring from vertex to rump 45 mm., the caecum measures 17 mm. In general arrangement there is no essential difference as regards the caecum and its appendages from *Cercaërtus*, as far as could be made out on rather poorly preserved material.

7. *Petaurus breviceps* Waterhouse. Short-headed Flying-Phalanger.

In *Petaurus* the general disposition of the gut agrees with that of *Trichosurus* and *Phalanger*. As found by Lönnberg, the ileum opens directly into the commencement of the colon by a prominent rounded “valve” surrounded by a sphincter, but lacking any related mucous retinacula. There is, however, a distinct caeco-colic sphincter immediately aboral to the “valve”.

The caecum, for the size of the animal, is very capacious. It describes a strong curve, convex to the right, with the greater curvature 55 mm. long. The curve is more exaggerated proximally, the distal two-thirds being less bowed. The sac is sausage-shaped, but narrows to a conical tip. The median mesotyphlon is extensive and has the same relation to the sinistral, vessel-bearing fold as in *Trichosurus*. About five large caecal branches spring from the principal caecal vessel. Another, recurrent vessel enters the free edge of the fold which forms the ventral wall of the deep ileo-caecal fossa.

8. *Petaurus papuanus* Thomas. Papuan Flying-Phalanger.

Several adult specimens of this species have been examined. Apart from the larger size of all parts, the arrangements are precisely as in *P. breviceps*. In an adult male the greater curvature of the caecum measures 75 mm. and the diameter is 8.5 mm. in the middle of the passage. The terminal third tapers rapidly.

The basal part of the median mesotyphlon projects as far to the left as the dorsal, vascular fold, which is thus obscured in the undisturbed state of the viscera. The sinistral artery is invariably the principal one.

9. *Dactylopsila melampus* Thomas. Black-footed Three-striped Phalanger.
(Pl. 5, fig. 17.)

In an adult male of this striped phalanger we find the large intestine arranged as in *Petaurus* and the caecum similar in position, shape and relative size (fig. 17). It differs, however, in having a reversal of the normal phalangerine arrangement of the related peritoneal folds and their associated vessels.

The main blood-supply to the caecum is derived from a morphologically dextral artery which raises a distinct fold from the ventral aspect of the mesenterium commune, proceeding across the ileo-colic junction, therein to gain the lesser curve of the caecum, along which it travels towards the tip. Dorsal to this fold is a more or less avascular, median fold, unconnected with the preceding, and separated therefrom by a distinct peritoneal fossa. The main vessel also supplies a branch direct to the caeco-colic junction, and this branch sends caudally another to form a loop with the first true caecal branch. Others are given to the proximal part of the colon, the first of these being raised in a fold, which guards a cranially directed peritoneal pocket—recalling that already described in *Isoodon* (p. 196). A sinistral caecal artery of small size proceeds subserously across the ileo-colic junction, and forms an anastomosis on the caecum with the main ventral (dextral) vessel.

In view of the uniformity in general arrangement of most of the other Phalangerinae, it is possible that our example of *Dactylopsila* presents individual variation such as that recorded by us (1948) in *Pongo*, *Homo* and *Aotes*, but it is not unique in the family or order.

10. *Schoinobates volans* (Kerr). Taguan Flying-Phalanger. (Pl. 5, fig. 18.)

In an advanced pouch-young female of this species (Royal Scottish Museum No. 991) the large intestine is much elongated, recalling that of *Vombatus*. It has a distinct hepatic or right flexure, followed by a short, straight transverse colon with relatively short mesocolon, and from there onwards a much coiled "descending" colon. The ileo-colic junction is oblique, and between it and the hepatic flexure is a short "ascending" colon. Opposite the ileo-colic junction, but slightly toward the caecal side, is a bulbous dilatation. Beyond this the caecum narrows to an elongated, much convoluted, cylindrical tube, which is almost as long as the large intestine. Its terminal third, or rather more, tapers gradually to a bluntly rounded tip. An extensive mesotyphlon connects the whole length of the lesser curvature of this caecum with the terminal ileum. Detailed arrangements of the peritoneal folds and their associated vessels present no departures from the typical phalangerine plan.

Subfamily *PSEUDOCHIRINAE*.

11. *Pseudochirus lanuginosus* Gould. South Australian Ring-tailed Phalanger. (Pl. 5, fig. 19.)

This Ring-tailed Phalanger shows a distinct advance on the conditions observed in the typical subfamily of phalangers, the advance pointing definitely in the direction of the Macropodidae.

The colon is relatively long, but narrow, and shows incipient feeble sacculation. There is, as in *Schoinobates*, a division into "ascending", transverse and "descending" colons, the last mentioned being much convoluted.

The caecum is a very capacious, curved sac, of considerably greater calibre than any other part of the intestine. It is, furthermore, distinctly sacculated and provided with two longitudinal taeniae, placed one dorsally and one ventrally.

From the right-angled ileo-colic junction it proceeds at first caudally, turning thence to the left, while the terminal third or more is folded back on itself like a catherine wheel. The apex forms a bulbous dilatation or minor sacculation (*vide* also Lönnberg, 1902). The arrangement recalls that of the peculiar "insectivore" *Galeopterus*.

The disposition of the mesotyphla also presents an evolutionary advance on the typical phalangerine conditions, of which they may be regarded as an exaggeration. The sinistral fold, carrying the principal or dorsal caecal artery, has now completely usurped the function of the median anangious mesotyphlon. The latter is reduced to a mere triangular vestige crossing the ileo-caecal angle. The cranial attachment of the principal mesotyphlon is along a broad line on the dorsal (sinistral) aspect of the enteric mesentery—as in typical phalangers. There is a short, thick, serous dextral fold transmitting a fairly big artery which sweeps on to the base of the caecum to form an arcade with the proximal branch of the sinistral artery. Further arcades are formed in the large mesotyphlon, and from these the terminal visceral arteries are derived.

Subfamily *PHASCOLARCTINAE*.

12. *Phascolarctos cinereus* (Goldfuss). Koala. (Pl. 5, fig. 20.)

The visceral arrangements of the Koala have long been known since the first description by Home (1808) and the later contributions by Knox (1826), Martin (1836), Owen (1841), Forbes (1881) and Young (1881), besides the accounts of the intestine given by Mitchell (1916), Lönnberg (1902), Oppel (1897), Sonntag (1921) and Mackenzie (1918).

There would seem, therefore, little to add, but we find that the descriptions given of the structures accessory to the caecum need further definition. We have examined the viscera of three adults.

In general disposition of the hind-gut and its mesenteries *Phascolarctos* is more typically phalangerine than is *Pseudochirus*. We can confirm the accounts of Forbes, Mitchell and Mackenzie. The colon is attached to the pyloric and proximal duodenal area by a fibrous suspension some 10 to 15 mm. long. This divides it into an oral and an aboral limb, both of which are elongated, convoluted and suspended in free mesocolic folds. The left or aboral limb is of small calibre, the right, shorter limb broadens when traced orally and terminates in the very wide and exceedingly long caecum. The ileo-colic union is roughly rectangular.

The caecum shows, according to Mackenzie, the "greatest instance of caecal development in the Mammalia", reaching a length of almost 250 cm. As regards size, this may be true, but it lacks specialization. It is smooth-walled, but greatly convoluted. Martin (1836 b), however, mentions a longitudinal muscle band along the attachment of the mesotyphlon and a tendency for the development of another on the opposite wall. We are inclined to regard these as temporary physiological phenomena rather than permanent structures. The organ narrows gradually towards its apex, which is bluntly conical, though there is some individual variation as to precise mode of termination. Internally there are no specializations, the mucosa being smooth and raised into ten or a dozen longitudinal rugae.

The caecum of *Phascolarctos* is provided with a huge mesotyphlon of falciform outline. Distally this is attached along the whole length of the lesser curve of the viscus. Proximally it springs from the dorsal aspect of the mesenterium commune some distance from the ileal border thereof, along an oblique line extending on the right to the ileo-colic angle. In the free falciform margin courses the principal caecal artery which supplies branches to the whole length of the caecum, as shown in fig. 20. No dextral vessels could be detected in our specimens, nor any trace of the anangious intermediate fold. Clearly this is an advance on the typical phalangerine condition, but in a different direction from that taken by *Pseudochirus*.

Family HYPSPRYMNODONTIDAE.

1. *Hypsiprymnodon moschatus* Ramsay. Musk Kangaroo. (Pl. 5, fig. 21.)

The anatomy of this rare Kangaroo has been dealt with by Carlsson (1915), and we have also had access, through the kindness of Prof. A. A. Abbie, to relevant extracts from an unpublished monograph on the genus by Dr. Ruth Highway. We have ourselves examined Owen's specimen, now in the British Museum.

As pointed out by Carlsson (1915), the large intestine is typically macropine in its arrangement, presenting a colon which is subdivisible into caecum, "ascending" colon, hepatic flexure, transverse colon, splenic flexure and "descending" and sigmoid colons. The flexures are very distinct, and in Owen's animal there are many secondary coils on the descending and pelvic portions. The whole colon is slung in an ample mesocolon, that of the transverse colon being adherent to the great omentum. There is a slight tendency to sacculation, but we find no specialization of the longitudinal muscular coat to form taeniae.

The caecum springs from the colon well posteriorly, due to the great length of the "ascending" colon. The terminal ileum has an almost directly caudad direction, with some inclination to the right, and from the ileo-colic junction the caecum curves sharply medially and then forwards in hook-like fashion. It is a simple blind sac with broad, rounded apex, but shows some tendency to sacculation on its major curvature. In Owen's animal the major curvature measures 48 mm. long: Highway (*loc. cit.*) gives the length as 50 mm. This worker found the lining to be slightly rugose in a longitudinal direction.

The blood supply of the caecum in *Hypsiprymnodon* is derived almost entirely from a large, single, sinistral caecal artery which crosses the ileo-colic junction in a thick, well-raised fold; this, traced distally, annexes the otherwise vestigial median mesotyphlon and proceeds therein to the apex caeci, lying close to the lesser curvature of the blind-gut. Immediately after emerging below the anti-mesenteric border of the ileum the caecal vessel gives a recurrent artery to the ileum, gaining that viscus by traversing the free edge of the median mesotyphlon. A small twig arises from the termination of the anterior mesenteric artery to supply the ventral wall of the gut opposite the ileo-colic junction, but this does not raise any vascular fold, nor does it gain the caecum.

Family MACROPODIDAE.

Subfamily POTOROINAE.

1. *Potorous tridactylus* (Kerr). Dark Rat-Kangaroo. (Pl. 6, fig. 22.)

Viscera from two adult females and two adult males of this species have been examined.

The large intestine is disposed much as in most marsupials, being bound down in the pyloric region and floating freely in its mesocolic supports to right and left, the whole forming a free arcade around the centrally bunched small bowel. In *Potorous* there are no secondary coilings of the colon, either on its oral or aboral limb. The oral limb, however, shows some specialization in its tendency to sacculation and the formation of slender taeniae coli. The ileo-colic junction forms a right angle.

The caecum is a capacious, but relatively short, sausage-shaped sac, of greater calibre than the colon and increasing in calibre from base to apex. The apex is therefore broad and rounded. It is smooth-walled throughout. There is only one true mesotyphlon, a short median triangular fold carrying merely a single recurrent vessel to the ileum. This may be marginal or a few millimetres from the margin if, as in one of our examples, the median mesotyphlon is more extensive.

The principal caecal artery is a sinistral vessel springing from the termination of the anterior mesentery and sweeping across the terminal ileum close to its junction with the colon, in a relatively low fold of peritoneum. It follows the lesser curve of the caecum to its apex, supplying firstly the recurrent ileal branch, which runs in the median mesotyphlon, and afterwards a series of annular vessels to the caecal wall, four or five on the ventral and six or seven on the dorsal wall. The basal area of the ventral wall is supplied by twigs from a short dextral artery which gains the caecum obliquely by crossing the ileo-colic junction in a short peritoneal fold which, in one of our specimens, was fatty. Both dextral and sinistral peritoneal vascular folds are sufficiently raised to produce peritoneal fossae beneath them.

2. *Bettongia cuniculus* (Ogilby). Tasmanian Rat-Kangaroo. (Pl. 6, fig. 23.)

In an adult female of this prehensile-tailed Rat-Kangaroo we find the alimentary system very similar in its general arrangement to that of *Potorous*, but there are many differences in detail. The colon, for instance, is provided with an elongated ansa on its transverse portion. On the oral side of this the "ascending" colon undergoes considerable dilatation, recalling that noted in *Phascolarctos*. The dilatation is progressive in character as far as the ileo-colic junction. Here the caecum continues in line with the colon, retaining the increased diameter until near its apex, the terminal third diminishing slightly in calibre. This caecum is relatively shorter than in *Potorous*, but otherwise very similar.

There is a short, thin, triangular, entirely anangious median mesotyphlon. This intermediate fold has a curiously oblique disposition, suggesting some differential growth in different parts of the wall of the terminal ileum—its ileal attachment

not being truly antimesenteric but pulled ventralwards out of its normal alignment (*vide* Pl. 6, fig. 23). In other respects the vessels are arranged almost exactly as in *Potorous*, gaining the caecal wall in short, thick, fatty folds associated with short peritoneal fossae.

Subfamily *MACROPODINAE*.

3. *Petrogale penicillata herberti* Thomas. Brush-tailed Rock Wallaby. (Pl. 6, fig. 24.)

The anatomy of *Petrogale xanthopus* was studied by Parsons (1896) who found an unsacculated caecum, six inches long, of greater calibre than the rest of the colon and joined to the terminal ileum, which enters at an acute angle, by a fold of peritoneum reaching to the caecal apex.

In a female specimen of 200 mm. vertex-rump length (presumably an advanced pouch-young) of *P. penicillata herberti* from Queensland, we find a simple, tubular caecum of 35 mm. long. We confirm Parsons' estimate as to the relative difference in calibre between caecum and colon, but the transition takes place to the aboral side of the ileo-colic junction and is fairly abrupt. There is no "ascending" colon. We also confirm the presence of an extensive mesotyphlon. Morphologically this appears to be a combined intermediate and sinistral structure, for it receives the large dorsal caecal artery, which runs between its laminae, close to the lesser curve of the caecum, to which it supplies half a dozen transverse branches as well as a vessel to the anti-mesenteric wall of the ileum. A minute dextral ileo-colic artery ends opposite the site of junction in the bloated proximal part of the colon. It does not gain the caecum or anastomose with the sinistral system.

4. *Dorcopsis muelleri* Schlegel & Müller. Brown Dorca Kangaroo. (Pl. 6, fig. 25.)

Garrod (1875) discussed the caecal anatomy of this Kangaroo under the name *Halmaturus luctuosus*. He compared it with *Hypsiprymnodon*, pointing out that in the Dorca the caecum and large intestine are smooth and unsacculated, whilst in *Hypsiprymnodon* there are longitudinal muscle bands. We did not confirm this latter finding. Garrod's Dorca had a caecum of two and a half inches long, with the circumference the same, compared with a large intestine thirty-two inches long, one-third the length of the small intestine—the same proportion as reported by Owen (1852) in *Dendrolagus*.

We have examined only an advanced female pouch-young of *Dorcopsis*. It measured from vertex to rump one foot in length. Its colon is much coiled in its left portion, but there is a short uncoiled "ascending" colon leading aborally to a relatively fixed region, so that there is no true transverse colon. The beginning of the ascending colon is dilated to form an oblate spheroid sac, partially divided by a depression along its mesocolic border. Traced orally the axis of this sac is continued into the axis of the short cylindrical caecum (46 mm. long), which depends towards the pelvis, with but little leftward trend. The ileum joins the caeco-colic junction obliquely, and is constricted at the point of insertion. There is

a feeble indication of sacculation in the shape of a transverse sulcus about a third the distance along its greater curvature. The apex is incipiently conical. There is an extensive mesotyphlon extending distally to the caecal apex, having a lunate free border. Morphologically it is a combination of intermediate and sinistral folds, for it carries the principal (dorsal or sinistral) caecal artery, which gives a single recurrent branch to the ileum about half-way across the length of the mesotyphlon. The parent vessel courses near the caecal wall. A distinct ventral vascular fold and subjacent pocket are present, but the contained vessel is exhausted on the ileo-colic region.

5. *Dendrolagus ursinus* (Schlegel & Müller). Black Tree-Kangaroo. (Pl. 7, fig. 26.)

This species has been previously studied by Owen (1852) and Mitchell (1916). We find, in an adult female, a fairly typical macropine arrangement of the hind-gut. There is a short "ascending" colon, rather obliquely disposed, slung upon a relatively short mesocolon. This is succeeded by a much coiled left colon, as in *Dorcopsis*. Proximally the ascending colon increases considerably in calibre, enlarging to form a fusiform sac opposite the ileo-colic junction, i.e. the sac differs from that of *Dorcopsis* in being contributed to partly by the caecum. Distally the caecum tapers gently to an almost pointed apex. There is no trace of a second accessory caecum, referred to by Mitchell and which he affirmed to be common in the Macropodidae, on the mesenteric side of the ileo-colic angle, nor have we observed it in any other macropod. Possibly an appearance suggestive of a caecal outgrowth may occur in certain states of constriction of the fusiform dilated portion of the proximal colon; if so, we have not met with the condition, but cf. Owen (1836) on *Vombatus* as mentioned above.

An extensive intermediate mesotyphlon exists in *Dendrolagus*, whilst to its dorsal side is a distinct but shorter fold carrying the large sinistral caecal artery. This vessel and its fold are for the most part independent of the median fold, but recurrent ileal branches are contributed to it. There is a distinct peritoneal fossa between the folds. There is a feeble dextral fold, and a short dextral artery courses subserously on to the oral part of the fusiform sac, much as in *Dorcopsis*.

6. *Protemnodon rufogriseus fruticus* (Ogilby). Bennett's Wallaby. (Pl. 7, fig. 27.)

The visceral anatomy of the wallabies and kangaroos has received attention from numerous anatomists, though few have considered the details which are being specially treated in the present contribution. The publications of Mitchell (1905) and Mackenzie (1918) are specially relevant.

The general arrangement of the hind-gut is much the same in all and agrees with what has been stated above in dealing with *Dendrolagus*. The colon, as pointed out by Mackenzie, is bound down by thick peritoneum in the pyloric region, this being well to the right of the median plane, due to the enlargement of the stomach, which in its general morphology parallels that of the leaf-eating monkeys of the family Colobidae. To the right or proximal side of this fixed region is a relatively short, wide "ascending" colon provided with a rather short

mesentery, but to the left (or aboral) side the colon is thrown into numerous coils and is retained by a very lax mesocolon, the cranial end of which is raised up as a distinct fold by the stem of the posterior mesenteric artery.

In young examples of Bennett's Wallaby the colon and caecum are of the same calibre throughout, but in mature animals we find the caecum and proximal colon to be almost double the diameter of the rest of the colon. The ileo-colic union is almost a right angle and is placed well caudally in the right flank, the caecum depending thence into the pelvis. The caecum is relatively short and wide, smooth-walled, cylindrical and with evenly rounded apex. It is tethered to the ileum by an extensive mesotyphlon, the caecal border extending to the apex. This membrane may contain fat, especially in its free edge—sure evidence of the existence of vessels between its laminae. Morphologically therefore it represents fused median and sinistral peritoneal folds, the dorsal caecal artery being the main supply to the blind-gut. There is, however, a well-developed dextral vessel which raises an appreciable fold over the ventral surface of the ileo-caecal angle, with a correspondingly developed "ileo-colic" fossa. This dextral artery arches over in the fold, with its convexity to the right. It therefore ramifies on the basal part of the caecum, as in many Primates, and forms a distinct anastomosis with the principal stem of the dorsal caecal vessel. We find this vascular arrangement constant in the numerous examples that have passed through our hands, but it is not present in any other of the wallabies and kangaroos which we have studied.

7. *Protemnodon irma* (Jourdan). Black-gloved Wallaby. (Pl. 7, fig. 28.)

In an adult male of this species we find the large intestine arranged essentially as in *P. rufogriseus*, but the first loop of the aboral limb of the colon is elongated and forms a recurrent ansa resembling that of many lemuroids, for its apex is directed to the right in the angle of the hepatic flexure. The "ascending" colon is rather shorter than in Bennett's Wallaby, and the ileo-colic junction correspondingly nearer the hepatic flexure and the ileal entrance rather more obliquely disposed. The caecum is also correspondingly longer, its length being partly due to the higher position of the ileo-colic union and partly to intrinsic elongation, for not only does the caecum depend vertically caudalwards into the pelvis, but its apex is upturned on itself. The total length of the greater curvature is 245 mm. The caecum increases slightly in calibre from base to apex, recalling that of *Macropus rufus*, and the reverse of that of *P. rufogriseus*.

The mesotyphlon is extensive, proceeding to the caecal apex, and exhibiting a falciform free border, which carries a recurrent ileal artery. An accessory recurrent ileal bisects the membrane more proximally. The main caecal artery is the sinistral vessel, which courses close to the lesser curvature. The dextral artery is abortive, terminating on the ileo-colic area and not raising any peritoneal fold.

8. *Thylogale eugenii* (Desmarest). Dama Wallaby. (Pl. 8, fig. 29.)

We have examined three adults of this species, a male and two females. All agree in the characters herein discussed.

The large intestine is, on the whole, simpler than in the other wallabies examined. It is uniformly wide in calibre and forms a simple arcade, with relatively few coils on the most aboral part of the left colon. There is a definite transverse colon with a short but distinct mesocolon, whilst the "ascending" colon, of moderate length, has a relatively free mesocolon. All the specimens came from captivity and the mesenteries are consequently all heavily fat-laden. The terminal ileum takes an oblique course cranially and to the right, the ileo-colic junction lying at about the mid-point of the right flank.

The relatively straight, wide, cylindrical caecum depends into the pelvis, retaining its calibre throughout and ending in a broad, rounded apex.

The mesotyphlon is a compound membrane closely resembling the typical phalangerine structure rather than that of the other macropods. The sinistral, vessel-bearing fold takes origin high up on the dorsal leaflet of the mesenterium commune, sweeping past the terminal ileum to fuse with the median mesotyphlon about half-way along the latter's length, and thereby supplying the caecum through the intermediacy thereof. There is also a well-marked fatty dextral fold crossing the terminal ileum transversely at the point where it inserts on the wall of the hind-gut. Its artery descends thence for some quarter of the distance along the ventral wall of the caecum, but forms no arcade or anastomosis with branches from the sinistral vessel.

In one of the female examples the caecum measured 75 mm. long and had a diameter of 20 mm.

9. *Macropus kanguru* (Müller). Great Grey Kangaroo. (Pl. 8, fig. 30.)

Two examples of this Kangaroo have been dissected for the present purpose, a subadult male and an adult unsexed.

We find, as did Mackenzie, that the caecum in kangaroos is larger, not only absolutely but also relatively than in any of the wallabies examined.

The disposition of the large intestine calls for no special remark as it is well enough known from the writings of others. The ileo-colic junction is very oblique, the last section of ileum proceeding almost vertically upwards. Thus the "ascending" colon is almost obsolete, but a large space is left for the elongation of the caecum. This is as wide or wider in calibre than the colon and is liable to be thrown into folds or spirals. When arranged flat, after removal from the body, it assumes a simple coil, due to its own intrinsic shape (i.e. great contrast between greater and lesser curvature) and also to the mode of tethering by the mesotyphlon. The apex, bent over on itself, is distinctly bulbous. The mesotyphlon is remarkably extensive. It carries the large sinistral or principal caecal artery. This courses rather nearer the caecal wall than the middle of the membrane, and is carried distally on to the bulbous fundus caeci. It gives no less than six recurrent ileal arteries. There is an obsolescent dextral vessel which supplies a very limited area of the ventral wall of the hind-gut opposite the ileo-colic junction. It is partially obscured by fat lobules which are sufficiently large to raise a slight dextral serous fold. A large anangious fold sweeps across from the ileo-colic angle to the right border of the large mesenteric lymphoid mass. This has a falciform free edge directed caudally.

10. *Macropus robustus* Gould. Wallaroo.

In this species, of which we have examined a single animal, an adult male, we find certain features at variance with the other large macropods. There is a capacious and elongated colon, the first part of which is quite markedly sacculated, due to the development of at least one well-marked, broad, longitudinal muscle-band running along the ventral aspect. A second is probably present along the mesenteric attachment, but obscured thereby. The sacculated region commences opposite the ileo-colic junction and affects the long "ascending" and transverse segments of the colon. The terminal colon is unsacculated and, as in other macropods, thrown into numerous coils. A mesocolon is present throughout the length of the colon.

The ileo-colic junction is much less oblique than in *M. canguru*, whence there is a good length of "ascending" colon.

The caecum is an elongated sausage-shaped viscus 22 cm. long, continuing caudally the line of the ascending colon. It is not, as in the other large macropods, upturned at its apex. The latter is rounded and smooth. In girth the organ is somewhat greater at its base (14 cm.) than elsewhere, but not so distended as the first two or more sacculations of the colon (18 cm.). The taenia coli is traceable for some distance along the ventro-lateral wall of the caecum, but does not appear to cause any sacculaton of the viscus.

The extensive mesotyphlon resembles that of *M. rufus*. It is vascularized by the large dorsal (sinistral) caecal vessels, from which several recurrent ileal branches are derived. Small dextral vessels are associated with the proximal colic vessels. They ramify over the wall of the colon and proximal caecum and neighbouring part of the terminal ileum at the junction of the three structures, anastomosing caudally with the most proximal caecal branch of the dorsal vessel. These ventral vessels raise no peritoneal fold over the ileo-colic junction, whereas the dorsal vessels form a large outstanding fold which crosses the terminal ileum to fuse with the dorsal aspect of the mesotyphlon.

11. *Macropus rufus* (Desmarest). Red Kangaroo. (Pl. 8, fig. 31.)

We have examined two specimens, both males, one adult and one juvenile. We cannot agree with the assessment of Windle & Parsons (1897) that the caecum is "straight and non-sacculated". This may be so after removal from the body and disruption of its peritoneal connections—for we found this to be the state in an inflated and dried specimen. When *in situ* the caecum is strongly curved and more than incipiently sacculated. It is not so elongate as in *M. canguru*, for the ileo-colic junction lies more caudally in the right flank, and there is a correspondingly longer "ascending" colon, and a very acute hepatic flexure. From the ileo-colic union the caecum sweeps caudally and medially in a strong arch, the final third being upturned. If laid flat on a table it forms about half the extent of a single spiral turn. The apex is blunt and rounded, slightly wider in calibre than the rest of the caecum, which is itself wider than the ascending colon. The length of the caecum in an adult is 275 mm., and the diameter of the order of 50 mm.

The caecal wall is throughout rather irregularly sacculated, from the presence of localized zones of constriction, but these may be only temporary phases, due to muscular activity. Some of the irregularity, however, cannot be so explained, because there is a very definite indication of the development of specialized longitudinal muscular bands. These are confined to the ventral face of the gut, and are not continuous throughout its length. A band on the basal part of the caecum loses itself about one-third the distance along the viscus; but a segment reappears over the strongly flexed region, separating the upturned apical segment from the body of the blind-gut. Opposite the ileo-colic junction the taenia is lacking, but it reappears aborally, forms a well-defined structure on the ventral wall of the ascending colon, but spreads out again, beyond the hepatic flexure, to form a complete investment on the aboral part of the transverse colon. The arrangements of the peritoneal appendages and vascularization of the caecum in the Red Kangaroo are essentially the same as in *M. kanguru*, apart from the proportionately smaller extent of the mesotyphlon in association with the shorter caecum. There is further a distinct indication in the vascular arrangements for the terminal upturned segment to receive a specialized artery of its own; this part appears to be supplied by the largest vessel—a continuation of the principal caecal artery which proceeds towards the sharp kink between the terminal segment and the main part of the viscus. Here it divides into two, its left branch coursing along the free margin of the mesotyphlon to supply the apex caeci, the right branch continuing to the caecal wall immediately to the right of the kink. The proximal parts of the caecum are supplied by a branch of the main vessel which runs parallel to its parent trunk, between it and the lesser curve of the caecum. It gives off numerous collateral branches to the caecal wall and terminates by anastomosing with the right terminal branch of the parent stem. Recurrent ileal branches are given off (*a*) by the principal caecal artery prior to its division (*b*) by the same vessel after its primary division and just prior to its terminal bifurcation. The last-mentioned courses in the free border of the mesotyphlon. A short dextral ileo-colic vessel corresponds to that of the Great Grey Kangaroo.

DISCUSSION.

I. MONOTREMATA.

For convenience the monotremes may be dismissed first. Manifestly the arrangements as regards morphology, physiology and development of the caecum and its appendages are so obviously different in this group from conditions in the marsupials that they have little bearing on the discussion concerning the latter.

The reduced caecum is clearly a primitive structure, having a simple form, small lumen and unimportant blood-supply. Physiologically it can be of little importance. Nevertheless its mere presence and the existence, at least in *Ornithorhynchus* and sometimes in *Tachyglossus*, of a vestigial vascular mesotyphlon suggests the possibility of a larger ancestral structure. At any rate, the condition in monotremes is a stage in advance of reptilian anatomy, but a direct comparison between the two conditions is difficult in the present state of knowledge of

the latter. Beattie (1926) directed attention to the question, but did not pursue the matter. From his studies and the earlier work of Lönnberg (1902 a) it appears that quite a number of lizards (for instance, *Amphisbaena*, most agamids and iguanids, e.g. *Metopoceros*, *Tupinambis*) bear intestinal caeca at the ileo-colic junction.* In all these, however, the blind sac is either lateral in position or on the mesenteric wall of the gut. The mesenteric position is judged by Beattie as being brought about by a differential growth-shift of a lateral caecum until it first of all impinges upon the homolateral leaflet of the mesentery and afterwards gets incorporated between the layers of the mesentery. What the relationship, if any, may be between these reptilian caeca and the monotreme organ—with its typically mammalian antimesenteric locus—is difficult to judge. The problem can only be solved, as Beattie believed, by study of ontogenetic stages in the various genera concerned. The following statement of Lönnberg seems to be relevant: "... I regard the polyphyletic origin of a caecum as likely. There is consequently, as far as I can see, no need to assume any direct genetic connection between, or common origin for such groups of vertebrates that possess a caecum on account of the presence of such organ." This may apply equally well to the pro-mammalians from which the monotremes presumably derive their origin.

The similarity of the caecum in all the monotremes precludes any correlation with diet, for the dietetic preferences of the Ornithorhynchidae and the Tachyglossidae could scarcely be more divergent. Moreover, there appear to be no compensatory and morphological differences elsewhere in the gut, beyond the presence of what Meckel termed valvulae conniventes in the jejunum of *Ornithorhynchus*, rendering it thus unique among subhominoid mammals.

II. MARSUPIALIA.

General : Factors determining presence and absence of caecum.

As a subclass the Metatheria, with the exception of the superfamily Dasyuroidea, are characterized typically by the presence of a caecum, frequently of large proportions. In the superfamily Dasyuroidea, with its two families Dasyuridae and Notoryctidae, the organ is constantly lacking. Two isolated genera from other families also lack a caecum, *Dromiciops* (Didelphidae) and *Tarsipes* (Phalangeridae). These are quite unrelated to the Dasyuridae or to each other, and both are therefore remarkable in so far as their nearest relatives possess caeca, some of them in a high state of differentiation.

Absence in the Dasyuroidea would *prima facie* appear to be correlated with the predominantly carnivorous propensities of the superfamily. No doubt disuse atrophy might be regarded as a potent factor in purely carnivorous species. In a vague way the position of the Dasyuroidea finds a parallel among eutherian families of the order Carnivora (especially the Ursidae, Procyonidae and Mustelidae). Examined more critically, however, there is less to be said in favour of disuse atrophy than appears on superficial observation. Not all Dasyuroidea are fully

* We have ourselves confirmed the presence of a small caecal appendage in several genera of lizards and have noted too its absence in *Varanus* and also in the rhynchocephalian *Sphenodon*.

and completely carnivorous, and it is doubtful if any are strictly so with the possible exceptions of *Thylacinus* and *Sarcophilus*. Many undoubtedly supplement their régime with insects and even vegetable food. *Myrmecobius* is a specialized formicivore and *Notoryctes* has similar habits to the eutherian moles. It is important to note also that it is in the less strictly carnivorous eutherian families that the caecum is absent, for it occurs, sometimes with its own specializations, in the Canidae, and is well developed in the most thoroughly carnivorous family—the Felidae. That morphology is more closely tied to phylogenetic or taxonomic status than to dietetic dictates is more fully evinced perhaps in the case of the Giant Panda (*Ailuropoda melanoleuca*) than any other. Here we have an aberrant procyonid that has become a specialized and strictly vegetable feeder, yet retains the typical procyonid gut with absence of caecum.

Some other factor therefore additional to a high protein diet is clearly involved in determining the loss of the caecum. At all events the inference may be drawn that once lost a caecum cannot be regained by secondary adaptation to a less exclusively carnivorous, omnivorous or even completely vegetarian diet. Examples such as *Myrmecobius* and *Notoryctes* and some of the smaller dasyuroids of the pouched-mouse type serve equally with the procyonids and bears to substantiate this argument.

Dromiciops and *Tarsipes* introduce other problems. *Dromiciops* appears to be the terminal member of an evolutionary series among the Didelphidae. In this series (*vide* fig. 2) a gradual transition can be observed between forms possessing a well-developed caecum, more or less characteristic of the family as a whole, and others with progressively smaller caeca, i.e. from *Didelphis*, through *Metachirus*, *Lutreolina* and *Chironectes* to *Dromiciops*. Presumably this series represents increasing specialization in one direction or the other; probably the end point in specialization here is the complete loss of the organ in *Dromiciops*. Insufficient is known as regards digestive physiology of the members of this family to make any definite pronouncements on their possible linkages with morphological status.

The problem is different as regards *Tarsipes*. No similar evolutionary series corresponding to that observed in the Didelphidae can be detected in the Phalangeridae, where, as a general rule, a large caecum is present. In fact we know of no other instance among mammals where the caecum is absent while developed to a relatively enormous degree in closely related forms (e.g. in *Trichosurus*). Moreover, in *Tarsipes*, the loss is not associated with an unusually simple colon or with a particularly complex stomach, as has been suggested by some other authors—presumably on the analogy of the well-known correlation between the state of the caecum and other parts of the gut as observed in Ungulata (*vide* Schliebich, 1929) where the metabolism of cellulose is the fundamental physiological requirement.

The very specialized feeding habits of *Tarsipes*—the diet being almost exclusively honey—would here seem to be the obvious explanation of any curious alimentary anatomical aberrations, although the mechanism of the association—the “efficient cause” in the language of logic—is not apparent. To find a physiological parallel one has to turn to birds where this restricted diet of honey or nectar is fairly

common, for instance, Meliphagidae, Nectariniidae, Trochilidae and certain psittacine genera.

Anatomically, however, as far as the caecum is concerned, these avian forms behave according to the morphological plan of their congeners; the Nectariniidae and Coerebidae, for example, possess the usual short caeca characteristic of passerines in general (Mitchell, 1901), although in *Promerops* they are practically obsolete (personal observation, W.C.O.H.). On the other hand, the honey-eating parrots and humming-birds lack caeca, but so also do other parrots, likewise the Cypselidae, which are by common consent regarded as the nearest relatives of the Trochilidae. Such specializations of the gut as exist in honey-feeding birds affect regions of the tube other than the ileo-colic (*vide* e.g. Steinbacher, 1934).

Peculiarities of diet may play a part in the reverse process of caecal hypertrophy. It is certainly true that in all vegetarian marsupials the caecum is capacious, either long, wide or both, and in several instances has other specializations super-added. Exclusive vegetarianism as such, however, would not appear to be a sole explanation of caecal hypertrophy. Some of the largest caecums among marsupials occur in species with an omnivorous diet (for example, *Trichosurus*). In the genus mentioned, and also in *Didelphis*, maintenance in health in captivity on a diet consisting mostly of raw meat and root-vegetables is feasible (Stones, personal communication) and a routine in most menageries.

Far too little is known, however, concerning the alimentary physiology (and particularly of such processes as cellulose digestion and absorption and water-absorption) in any of the marsupials for the true appraisal of such variations that occur as factors bearing on the morphological problem. Observations on the rates of alimentary transit, character of the faeces, whether hard, soft, pulpy or semifluid, etc., would no doubt result in the accumulation of valuable data for such appraisal, especially in view of the statements of Mangold (1929).

Form of the caecum.

The absolute and relative size and calibre of the viscus varies much—from such an elongated, capacious organ as that of *Trichosurus* to the abbreviated, wide one of *Echymipera* or the narrow vermiform structure of *Vombatus*. Slight curvature is common, e.g. *Perameles*, but, in many forms, one wall is much longer than the other, resulting in coiling. This is seen best, of course, in *Phascolarctos*, but it is also present in *Trichosurus*, and in *Macropus cangaru*, less obvious in *M. rufus*, and almost absent in other members of that group. Tendency to spiral twisting also occurs in *Phascolarctos*.

In one family, the Peramelidae, another evolutionary series is exhibited as regards size and specialization of the caecum. Here the most complex is *Macrotis*, then come *Perameles* and *Isodon* in turn, while *Echymipera* has the simplest arrangement. Presumably *Echymipera* here represents the primary stage, as not only is the caecum smaller than the others but its mesotyhylon is represented by a single median anangious fold, the flanking vessels being small, failing to raise up folds of peritoneum.

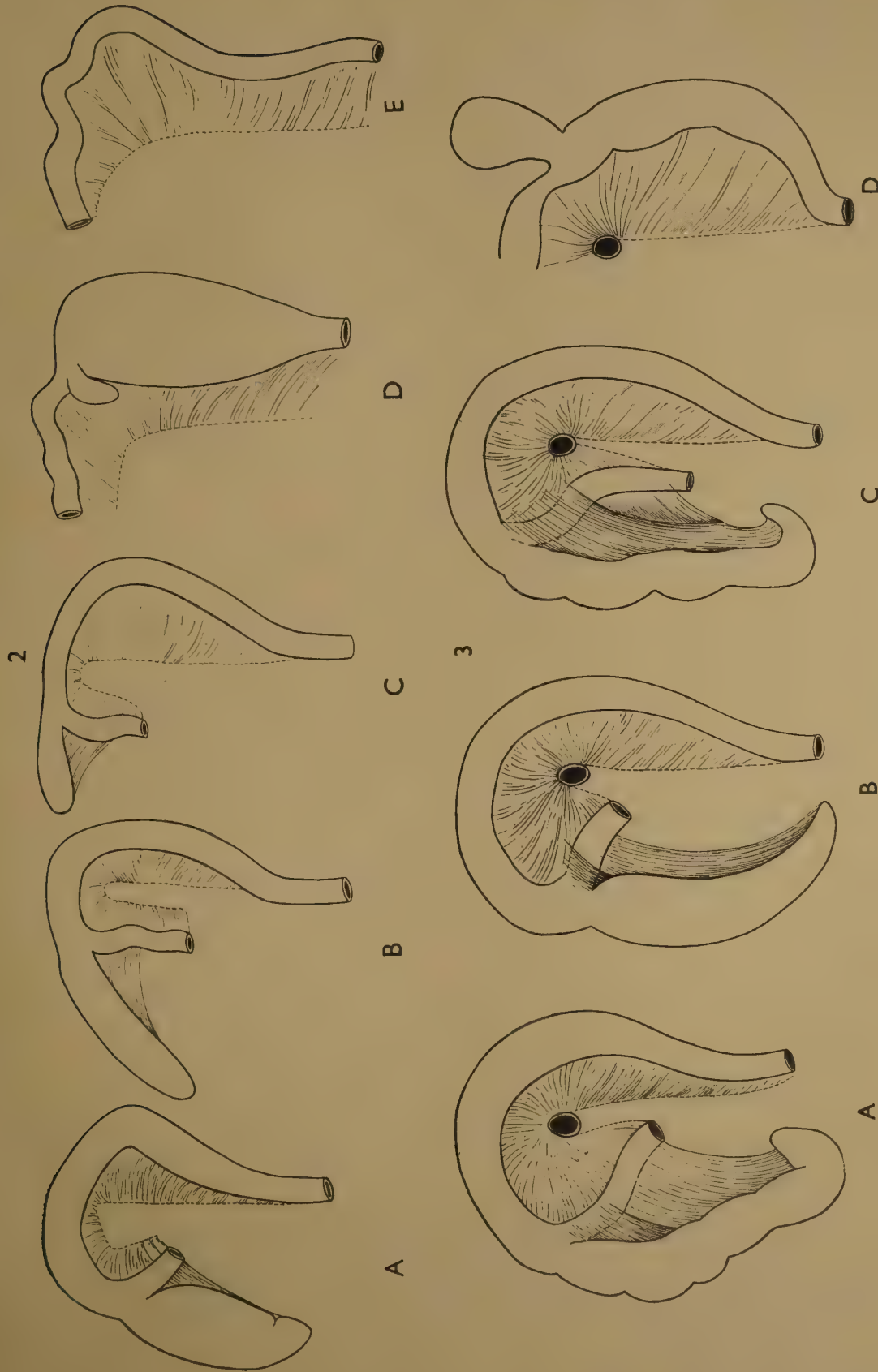


Fig. 2.

Series of diagrams to show the progressive decrease in the caecum in the genera of Didelphidae.

A, *Didelphis marsupialis*; B, *Metachirus*; C, *Lutreolina*; D, *Chironectes*; E, *Dromiciops*.

Fig. 3.

Diagrammatic figures to show an evolutionary series on the development of the caecum in the marsupial family Peramelidae.

A, *Macrolophus lagotis*; B, *Perameles nasuta*; C, *Isodon obesulus*; D, *Echymipera*.

In the two remaining large families, the Phalangeridae and the Macropodidae, differences in caecal size and form do not appear to fall into any consistent series, although there are in detail definite similarities between the members of each; for example, among the Phalangerinae, the sinistral arrangement of the blood-supply, coupled with the occurrence of vessels utilizing the primary mesotyphlon as a pathway, is correlated with enlargement of the viscus in such genera as *Trichosurus*, *Phalanger*, *Acrobates*, *Petaurus* and *Schoinobates*. A possible evolutionary series representing three stages in caecal specialization may be represented in the Phalangeridae by say *Dactylopsila*, *Trichosurus* and *Pseudochirus*.

Specialization of the external coat of longitudinal muscle to produce sacculaton is not so well marked as in the Primates, nor is it altogether a function of size. Thus sacculaton is absent in *Didelphis*, but is incipient in *Trichosurus* and *Phascolarctos*. *Isoodon*, *Hypsiprymnodon* and *Dorcopsis muelleri* also show some traces of sacculaton, albeit slight. In *Macropus rufus* longitudinal taeniae are obvious, but they can scarcely be said to be well developed. Their presence has also been affirmed in *Phascolarctos* and other genera, though possibly they are here transitory. The marked asymmetry coupled with sacculaton, seen in the caeca of so many of the higher Primates, is not found in any marsupial.

Proximo-distal specialization of the viscus occurs in a number of genera, resulting in a narrowed or upturned apex. Some simple narrowing towards the apex is found, for example, in *Petaurus* and *Bettongia*. This is never, however, so sudden as to produce a true vermiform appendix at the end of a cylindrical or conical caecum, as is seen in the Hominoidea, nor is it particularly well marked in the few forms where sacculaton is evident. Turning-up of the tip is frequent. Perhaps the simplest is *Didelphis*, in which there is little more than a constriction near the tip on the morphologically dorsal surface. In *Isoodon* and *Macrotis*, which are closely related, constriction and upturning are more evident, the former having the more pointed tip. In both cases the main vessel-bearing fold of peritoneum runs right along to the apex and the incipient sacculaton ceases well proximad of the constriction. This arrangement recalls the condition in *Daubentonina*. It is thus evident that no true appendix caecalis is to be found in any marsupial, nor for that matter in the monotremes. It is of some significance in connection with terminal specialization that in *Macropus rufus* the upturned apex has a separate blood-supply.

A curious simplification is noted in *Caenolestes* and in *Echymipera*; namely, a caecum whose long axis is directed cranially. In both cases the whole plan of the intestine, especially that of the large intestine, is a primitive one. Their caeca, however, differ; though small and rounded, that of *Echymipera* has three serous folds associated with symmetric dorsal and sinistral arteries, while *Caenolestes* has an anangious median fold and a vascularized dextral fold only. We can suggest no explanation for the cranial direction of the caecum, nor for its distribution apparently at random among forms so widely separated and with nearest relatives having the "normal" arrangement. Many other mammals with a primitive gut have caeca directed caudally, e.g. *Tarsius* in Primates and *Chironectes* in marsupials. Another curious proximo-distal differentiation is that found in some didelphids,

where there occurs a more or less extended basal constriction, coupled with distal ballooning. There is some tendency to annular constriction in all the didelphids that possess a caecum, e.g. *Didelphis* and *Metachirus*, but in *Lutreolina* this becomes an extended zone affecting, in some individuals, or possibly in certain physiological phases, about half the total length of the tube. The basal constriction is also noteworthy in *Echymipera*.

Blood-supply.

Marsupials show marked variation in the blood-supply of the caecum, especially as to which is the larger artery. They are thus in contrast to the Primates, where the principal artery is nearly always sinistral. For certain species our material is scanty, but experience has shown us how constant is this feature, although details of vascular arrangement are not usually considered to be constant characteristics. Among marsupials we have found the sinistral to be the main artery in the following forms: *Didelphis marsupialis*, *D. paraguayensis*, *Marmosa mitis*, *Lutreolina crassicaudata*, *Vombatus mitchelli*, *Trichosurus vulpecula*, *Phalanger orientalis*, *Acrobates pygmaeus*, *Petaurus breviceps*, *P. papuanus*, *Schoinobates volans*, *Pseudochirus languinosis*, *Phascolarctos cinereus*, *Hypsiprymnodon moschatus*, *Potoroës tridactylus*, *Bettongia cuniculus*, and all the Macropodinae, this last being the only one of the larger families in which *all* the members have the same bias in the blood-supply.

In some there appears to be no dextral artery at all, e.g. *Phascolarctos*, while in others it is very small, raises up no fold and may not even reach the caecum, terminating by supplying a segment of the ileum or colon or a small area of the caecal base, e.g. *Hypsiprymnodon* or *Protemnodon*. In others, however, the dextral vessel is relatively large, raises a well-marked peritoneal fold and may anastomose with the sinistral artery.

In one form only (*Echymipera*) do we find both arteries and both vascular folds to be of the same size.

The dextral is the main vessel in the following species:—*Metachirus opossum*, *Caenolestes fuliginosus*, *Perameles nasutus*, *Macrotis lagotis*, *Cercaërtus nana*, *Eudromicia caudata*, *Dactylopsila melampus*. There seems to be more specialization when this happens, as it is the only one found in several species, e.g. *Macrotis lagotis*, *Cercaërtus nana*. In other examples the companion artery is also well-developed and generally anastomoses with the main one, e.g. *Caenolestes fuliginosus* or *Metachirus*, in which it even bears recurrent branches.

There seems to be no definite reason why one or other artery should be the predominant. As already remarked, only in the Macropodinae do even phylogenetic factors appear to determine this point.

The mesotyphlon.

As observed in the introduction and further emphasized in the descriptive accounts, we find that the marsupial mesotyphlon typically falls into the threefold type-scheme of median anangious and paired flanking vascular folds. The most

generalized is *Echymipera*, which is almost diagrammatic of the ideal scheme. In all other genera the median fold is present in some degree, but the flanking folds are more or less modified, largely by the size of the arteries they carry and by such other "mechanical" factors as the distance proximal to the ileo-junction at which they cross the ileum and the angle they make with its longitudinal axis. Where one artery is missing or very small the corresponding fold is also missing or very small. Thus there is no dextral fold in *Phascolarctos* which lacks the dextral artery. In *Protemnodon* the dextral artery is very small and terminates in the ileo-colic area, so that no fold is raised. *Macropus kanguru* has a dextral fold which is barely distinguishable, while in the closely related *Thylogale eugenii* it is of intermediate size.

In discussing this feature in Primates we adopted the opinion that such "mechanical" factors were a satisfactory explanation of the facts, but in the marsupials this is evidently not the whole story. This is apparent when the relative size of the membranes of large caeca is considered, especially as regards the relative proportions of the median fold and that bearing the principal artery. The three relatively largest caeca are found in *Phascolarctos*, *Trichosurus* and *Didelphis* in descending order of size, although all the Phalangerinae as well as *Pseudochirus* also have large ones. However, as already emphasized, the enormous caecum of *Phascolarctos* appears to have only one correspondingly large peritoneal fold, the median. This is far from being anangious, since the main vessel uses it as a pathway. In the phalangers, and more particularly in *Pseudochirus*, the median fold is much reduced, though is still recognizable, as also is a small fold for the less important dextral artery. The main fold of attachment of the caecum, however, is the sinistral one, which bears the vessels. In *Pseudochirus* this is distinct from the median fold, but in *Trichosurus* and *Petaurus* the median and sinistral fuse to form one large sheet. In *Phalanger orientalis* the two remain separate for a greater part of their extent than in *Trichosurus*. *Cercaërtus* and *Dactylopsila* are, of course, unusual among phalangers in having only intermediate and dextral folds, the latter being the larger and carrying the artery of supply. In *Didelphis* and its allies yet a third arrangement is seen. Here the median fold is the largest, while the main artery enters it from a small sinistral fold. A small dextral fold is present and carries an artery which supplies part of the base of the caecum only. It communicates with the sinistral artery—now running in the median mesotyphlon—but does not enter that membrane.

It would seem, therefore, that factors other than purely "mechanical" determine which shall be the largest fold and that once this is determined the main arteries are transmitted to it. In the case of the intermediate fold they have to reach it by passing to one side or other of the ileo-colic junction and so demand a subsidiary fold. The median fold is the most persistent, some vestiges being present in all forms described, with the notable exception of *Phascolarctos*—which fact must surely be regarded as another specialization in this bizarre animal. It is in those forms with a long, narrow caecum, e.g. *Vombatus*, or where an appendix caecalis is present, e.g. the Hominoidea, that the principal vascular fold is longest, although not necessarily the largest.

SUMMARY.

1. A description is given of the caecal region of the gut in a number of monotremes and marsupials, covering most genera, some of which are now very rare and possibly even extinct. As in a previous memoir, particular attention is given to the peritoneal folds attached to the viscus and to its blood supply.

2. Monotremes exhibit a simple caecum tethered by a single median fold, or none (e.g. *Zaglossus*).

3. Marsupials as a group show a more complex arrangement, although, as in Primates, the caecum is typically anchored by a median anangious fold with flanking vascular folds on the morphologically sinistral and dextral sides. However, many complex specializations exist to modify this arrangement. One artery is typically the larger, and this is more often the sinistral than the dextral.

4. The size of the caecum may possibly depend on some factor in the diet of the animal, but this cannot be simply the proportion of vegetable material it contains, nor is it the only factor concerned.

5. Specialization within the viscus occurs in many marsupials, but never proceeds so far as to form an appendix caecalis.

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PLATE I.

PLATE 1.

- Fig. 1. *Ornithorhynchus anatinus*, ♀. Ileo-caecal region and large intestine from the ventral aspect, with related peritoneal membranes and associated vessels and lymphatic glands. Note the restriction of extraperitoneal fat to the transverse part of the mesocolon.
- Fig. 2. *Tachyglossus aculeatus*, ♂. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 3. *Zaglossus bruijnii*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 4. *Didelphis marsupialis virginianus*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect.

1, intermediate mesotyphlon; D, dextral caecal artery; Du, duodenum;
Lg, lymphatic glands; S, sinistral caecal artery.



PLATE 2.

PLATE 2.

- Fig. 5. *Didelphis paraguayensis*, ad. Ileo-caecal region and large intestine from the ventral aspect. Note the left colic loop.
- Fig. 6. *Metachirus opossum*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect and, below, the caecal region from the dorsal aspect.
- Fig. 7. *Lutreolina crassicaudata*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect and, below, the ileo-caecal region from the dorsal aspect.
- Fig. 8. *Myrmecobius fasciatus*, ♀ ad. General view of the abdominal part of the alimentary canal from the ventral aspect. Note simplicity of arrangement and absence of division between large and small intestine; also absence of caecum and presence of large ligamentum colico-duodenale.
- Fig. 9. *Caenolestes fuliginosus*, ♀ ad. Ileo-caecal region from the ventral aspect.
- l, intermediate mesotyphlon; CD., colico-duodenale; D, dextral caecal artery; Du, duodenum; LL., large intestine; MC., mesocolon; R, recurrent ileal artery; S, sinistral caecal artery; SI., small intestine.

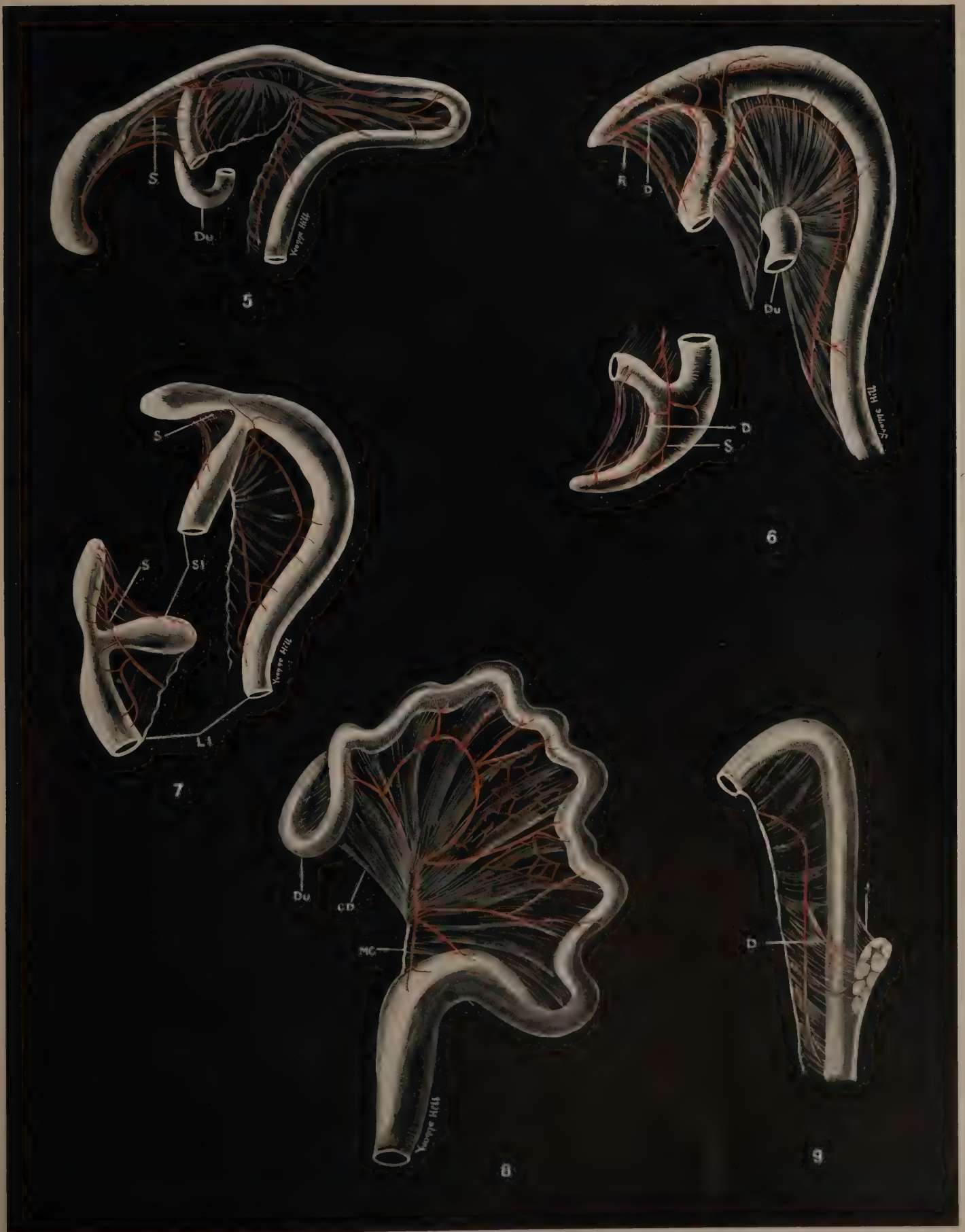


PLATE 3.

PLATE 3.

- Fig. 10. *Isoodon obesulus*. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 11. *Perameles nasuta*, ♀ ad. Ileo-caecal region and large intestine with associated peritoneal membranes from the ventral aspect.
- Fig. 12. *Macrotis lagotis*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 13. *Echymipera aruensis*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect.

1, intermediate mesotyphlon ; 3, dextral mesotyphlon ; D, dextral caecal artery ; Du, duodenum ; F, fold raised by proximal colic artery ; S, sinistral caecal artery.



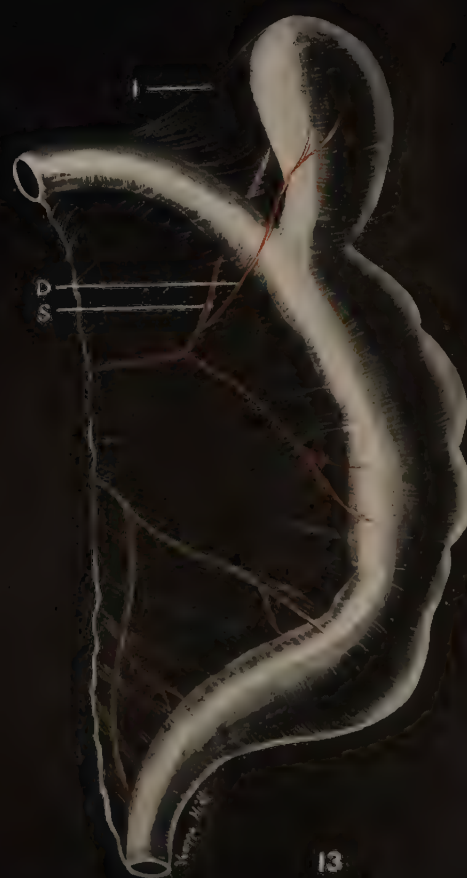
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PLATE 4.

PLATE 4.

Fig. 14. *Vombatus mitchelli*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect. The inset figures show details of the caecum and related parts : A, from the ventral ; and B, from the dorsal aspect.

Fig. 15. *Trichosurus vulpecula*. Ileo-colic region from the ventral aspect. Below, a more medial view of another specimen.

Fig. 16. *Cercaërtus nana*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect.

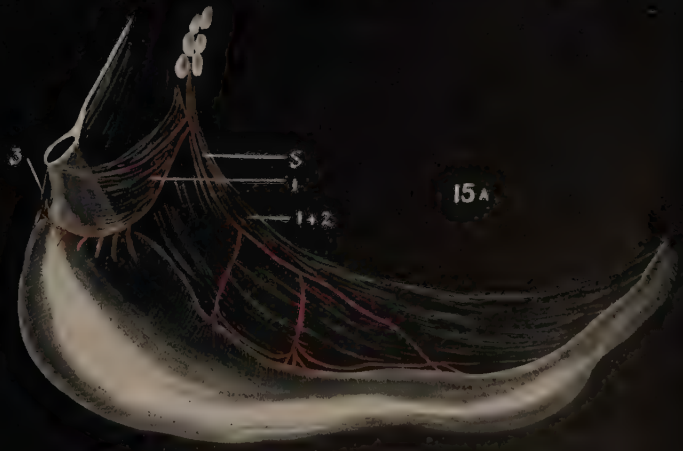
1, intermediate mesotyphlon ; 2, sinistral mesotyphlon ; 3, dextral mesotyphlon ; D, dextral caecal artery ; Du, duodenum ; Lg, lymphatic glands ; M, meso-appendix derived from dextral mesotyphlon ; S, sinistral caecal artery ; V, vessel in line of fusion of intermediate and sinistral mesotyphla.



14.



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15A



14A



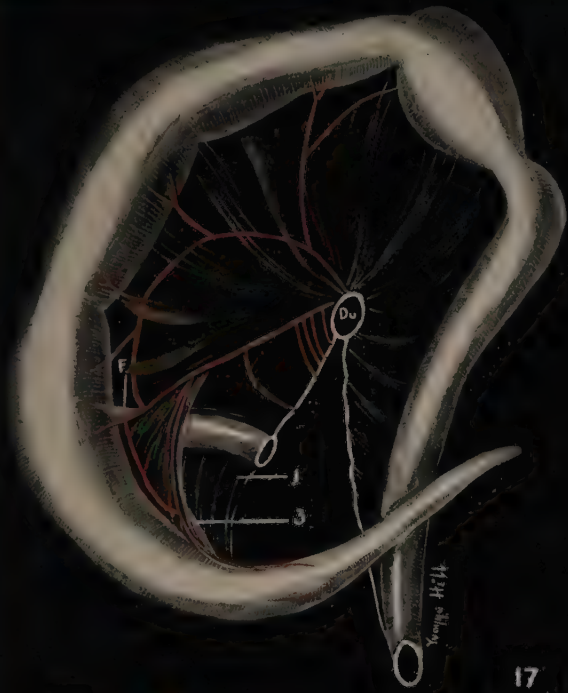
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PLATE 5.

PLATE 5.

- Fig. 17. *Dactylopsila melampus*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 18. *Schoinobates volans*, ♀ advanced pouch-foetus. Ileo-caecal region and large intestine with associated mesenteries, from the ventral aspect.
- Fig. 19. *Pseudochirus lanuginosus*. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 20. *Phascolarctos cinereus*, ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 21. *Hypsiprymnodon moschatus*. Ileo-caecal region and large intestine from the ventral aspect.

1, intermediate mesotyphlon ; 2, sinistral mesotyphlon ; 3, dextral mesotyphlon ;
D, dextral caecal artery ; Du, duodenum ; F, fold raised by proximal colic artery ;
S, sinistral caecal artery.



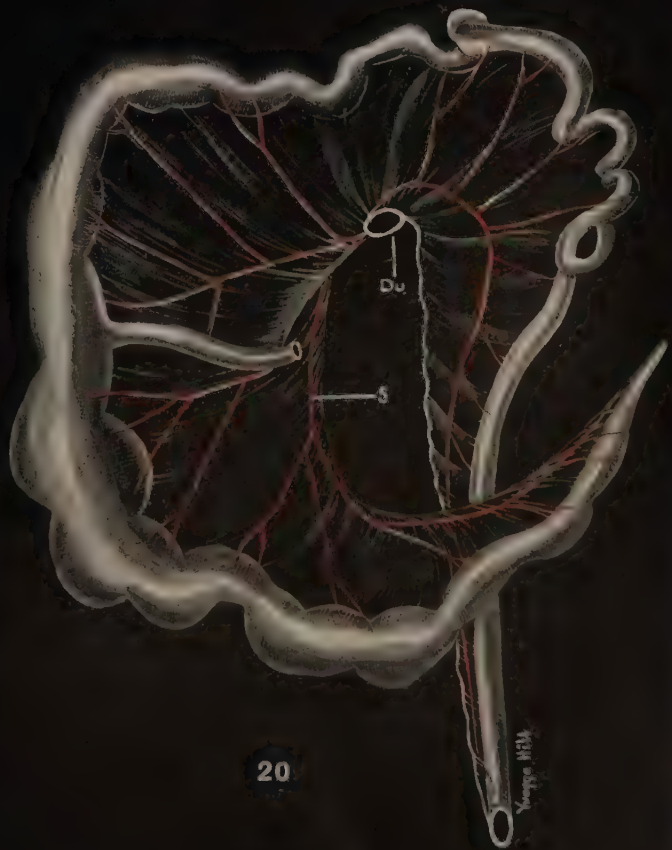
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PLATE 6.

PLATE 6.

- Fig. 22. *Potorous tridactylus*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 23. *Bettongia cuniculus*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect. Inset shows a medial view of the caecum to indicate the ileo-caecal fossa.
- Fig. 24. *Petrogale penicillata herberti*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 25. *Dorcopsis muelleri*, ♀. Advanced pouch-foetus. Ileo-caecal region and large intestine from the ventral aspect.
- 1, intermediate mesotyphlon ; 2, sinistral mesotyphlon ; 3, dextral mesotyphlon ;
D, dextral caecal artery ; Du, duodenum ; (F), to indicate the ileo-caecal fossa ;
S, sinistral caecal artery.

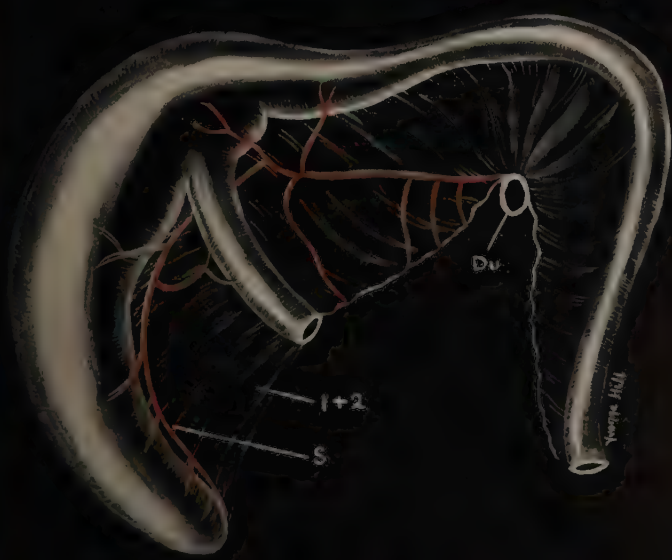
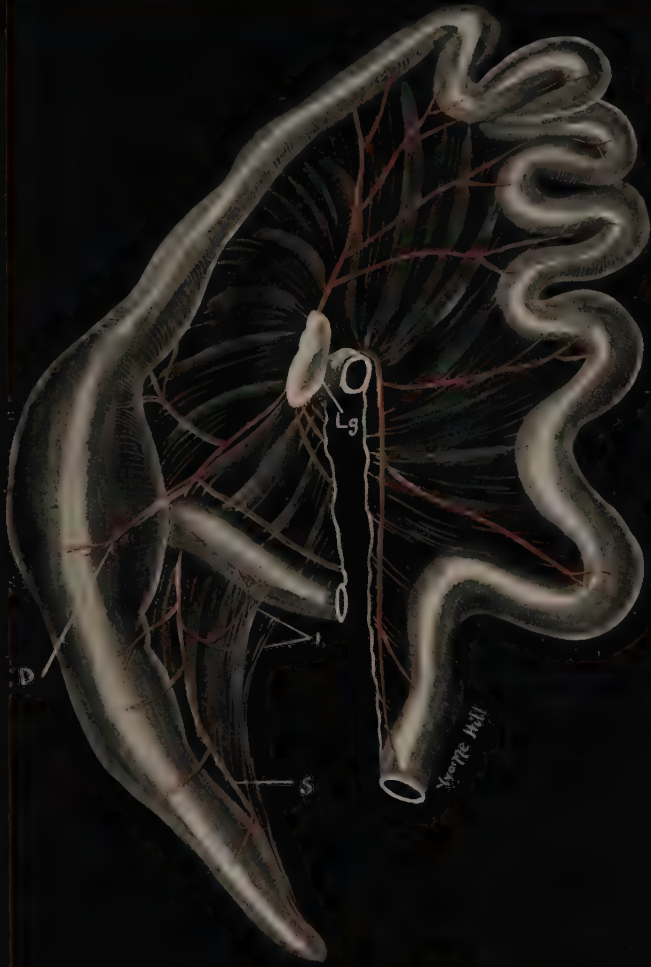


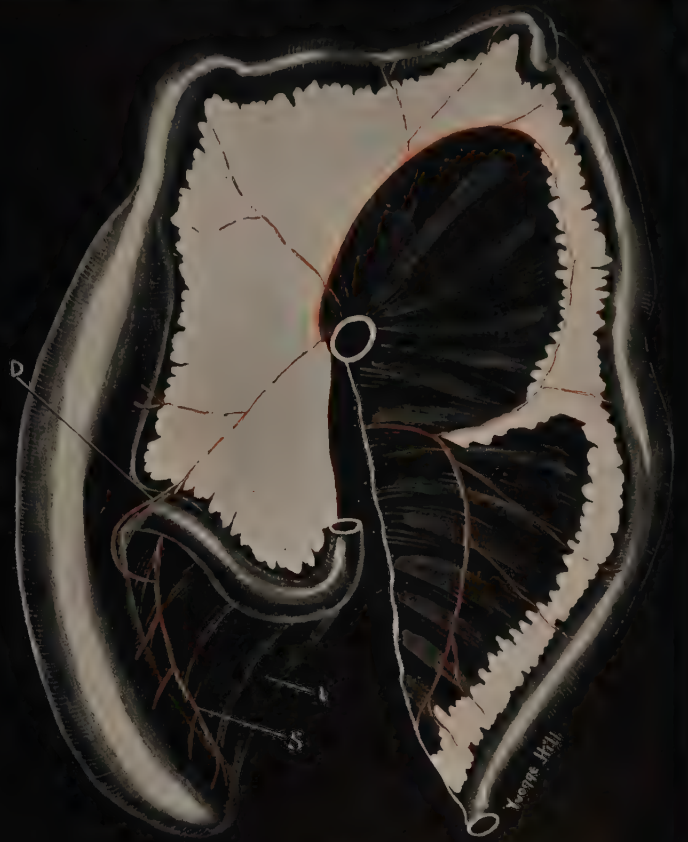
PLATE 7.

PLATE 7.

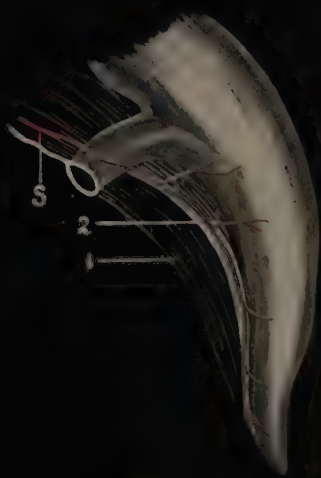
- Fig. 26. *Dendrolagus ursinus*, ♀ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 27. *Protemnodon rufogriseus fruticus*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect.
- Fig. 28. *Protemnodon irma*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect.
- 1, intermediate mesotyphlon; D, dextral caecal artery; Lg, lymphatic glands;
R, recurrent ileal artery; S, sinistral caecal artery.



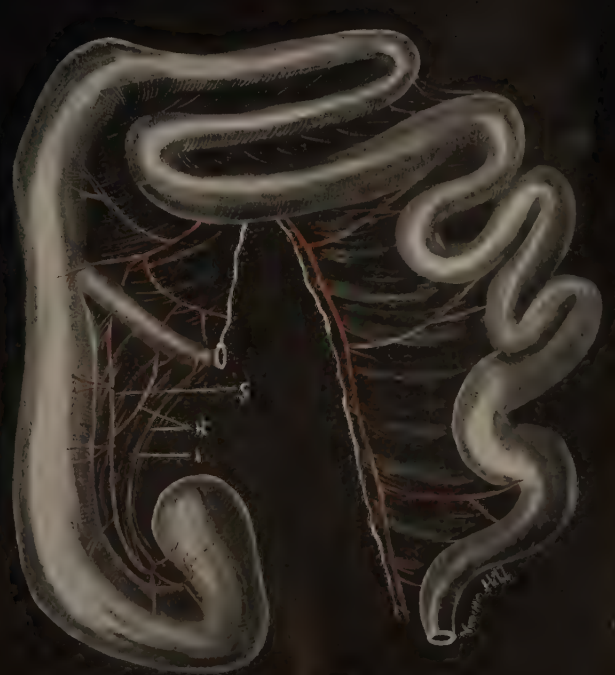
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26A



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PLATE 8.

PLATE 8.

- Fig. 29. *Thylogale eugenii*, ♂ ad. Ileo-caecal region and large intestine from the ventral aspect. Inset shows a medial view of the caecum.
- Fig. 30. *Macropus canguru*, ♂ subad. Ileo-caecal region from the ventral aspect. R indicates the most distal of a series of recurrent ileal branches from the principal caecal artery.
- Fig. 31. *Macropus rufus*, ♂ juv. Ileo-caecal region and large intestine from the ventral aspect.
- 1, intermediate mesotyphlon ; D, dextral caecal artery ; Lg, lymphatic glands ;
R, recurrent ileal artery ; S, sinistral caecal artery.



Development of the skull and associated structures in the Amphibia with special reference to the urodeles.

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(With Plates 1-3 and 27 figures in the text.)

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INTRODUCTION AND HISTORY.

This work is a general investigation of the head of the urodele *Cryptobranchus japonicus*, traced through a series of larval stages. This species was first reported by von Siebold (Temminck & Schlegel, 1838), hence its synonym *Sieboldia* (Parker, 1882).

The first description of the general adult anatomy of both soft and hard parts, including the brain and cranial nerve origins, seems to be that by Schmidt, Goddard & Van der Hoeven (1864). In 1865 Hyrtl described the adult skeleton and soft parts, and Fischer (1864) described the skull, muscles and nerves in *Cryptobranchus* and *Menopoma*, an allied American species. In 1869 St. George Mivart published some information about the myology of *Menopoma alleghaniensis*, Humphry (1872) studied

the muscles and nerves of *Cryptobranchus japonicus*, and Wiedersheim (1877) and Parker (1882) both described the adult skull and hyobranchial skeleton in the Japanese species. The first Japanese to publish information on *Cryptobranchus japonicus* was probably Sasaki (1877), but the most complete account of the adult anatomy is that of Osawa (1902). His descriptions include all systems of the adult.

Drüner (1904) described the hyobranchial skeleton, muscles and nerves in many urodeles, including the adult *Menopoma* and *Cryptobranchus japonicus*; Okasima (1906) described the inner ear of the adult *Cryptobranchus*. The early development of *Menopoma alleghaniensis* was described by Bertram Smith (1906, 1907, 1912); the early development of the egg of *Cryptobranchus* was investigated by de Lange (1906-16).

The next phase in the history of the investigations of *Cryptobranchus* was the study of the larvae. Edgeworth (1920) described the development of the urobranchiale in *Menopoma* while investigating the larval musculature, and in 1923 he described the chondrocranium in *Cryptobranchus* (37 mm. larva) and *Menopoma alleghaniensis*. The same year (1923 b) he described the larval hyobranchial skeleton and musculature in these animals. In 1928 Murayama described the development of the ear, Fukuda (1928) described the development of the hyobranchial cartilages, and Miyawaki (1929) studied the ear capsule.

Aoyama (1928, 1930) comprehensively studied the development of the sclerotic cartilages and the skull from larva to adult. However, his 1930 paper on the skull deals with skeletal structures only and he mentions little about nerves, blood vessels and musculature. The development of the nasal organs was investigated by Kawagoe (1932).

The present work describes the topographical relationships of the neuromuscular, blood, and muscle systems to the cartilage and bone. The most significant results obtained relate to the branchial region. Here there is displayed a segmental pattern of serially homologous elements, i.e. branchial nerves and muscles. The evidence suggests that vestigial branchial segments posterior to the fourth gill cleft were present and complete in some pre-amphibian ancestor. The glossopharyngeal and seven vagus branchial nerves and their related levatores arcuum branchialium muscles, together with the branchial elements and gill clefts have been analysed in some detail; their phylogenetic significance is considered at length. Furthermore, the facts suggest that the dilator-laryngeus and the trapezius muscles can be homologized with levatores VII and VIII, and it is tentatively suggested that the lungs in the urodeles are formed from the seventh branchial segment.

MATERIAL AND METHODS.

A series of stages of larvae of *Cryptobranchus japonicus* (*Megalobatrachus maximus*) measuring 15, 17, 19, 26, 30 and 32 mm. in total length after fixation were examined. The larval heads were investigated from transverse sections and the arrangement of the various structures was graphically reconstructed from lateral and ventral views. To provide a frame of reference for the reconstructions it was assumed that the trabeculae cranii and the basal plate lie in one plane. In the earlier larval stages the mid-line of the brain up to the pituitary is assumed to be straight. The series of larvae examined were obtained from a small collection which had been preserved in the Department of Embryology, University College London, since 1923. This collection included some early eggs and thirteen larvae (ranging from 12 mm. to 32 mm. in total length) of *Cryptobranchus japonicus*. These larvae were listed as having been received from Dr. Ishikawa of Tokio. The material had probably been fixed in Zenker's fluid; it was

preserved in 70 per cent alcohol. Serial sections ten microns thick were cut transversely, all the sections except those of the 32 mm. stage being stained with Heidenhain's azan carmine stain; the 32 mm. stage was stained with Weigert's haematoxylin and counterstained with Pasini. On the whole the Heidenhain's azan stain gave the more satisfactory results. With it the neurilemmal sheaths of the peripheral nerves are stained light blue and can be distinguished from the surrounding tissue. The cartilage and bone cells are stained light and dark blue respectively. With Weigert's and Pasini's stains the neurilemmal sheaths are more difficult to follow. The descriptions of the nerves are concerned with topographical relationships; the condition of the material did not allow any detailed examination of nerve components with the central connections inside the brain.

DETAILED DESCRIPTIONS.

(a) The 15 mm. stage larva.

General features.

The ectoderm and dorsal root ganglia are almost clear of yolk; the endoderm cells and the developing muscles contain much yolk. The lateralis, epibranchial and crest constituents of the ganglia cannot easily be distinguished from one another. There is an open communication between the primary optic vesicle and the fore-brain and the lens still contains a cavity. Rudiments of the eye muscles in the form of yolk mesenchyme lie dorso-medial to the eye. Ventral to the eyes, the nasal sacs have a small cavity leading to the exterior by a fairly large aperture. There is no mouth opening nor open gill clefts, though the spiracular (hyoid) pouch lies very close to the ectoderm (Pl. 1, fig. 3). The trigeminus musculature runs postero-ventrally from the postero-dorsal surface of the eye beneath the gasserian ganglion. The facial musculature arises beneath the auditory sac and spreads behind the hyoid pouch. This stage is roughly comparable to stage 4 (approx. 7 mm. total length) in *Amblystoma mexicanum* (Starck, 1937).

Neuromuscular system.

The ophthalmicus profundus ganglion lies dorsal to the eye; it is elongated dorso-ventrally, continuing vertically downwards as the ophthalmicus profundus nerve which is distributed to the skin antero-lateral to the nasal sac (Pl. 1, fig. 2; text-fig. 1). Postero-dorsally this ganglion is continuous with the gasserian ganglion but there is a suggestion of a border between them. This border cannot be distinguished in later stages (text-fig. 1).

The gasserian ganglion lies against the mid-brain. It is approximately spherical in shape and slightly larger than the ophthalmicus profundus. A large r. mandibularis V is a postero-ventral prolongation of the gasserian ganglion. This nerve lies latero-dorsal to the trigeminus musculature and is intimately associated with it. A r. maxillaris V is not present. The r. mandibularis V lies mesial and extremely close to the dorso-ventrally running lateralis r. buccalis VII (text-fig. 1). Whether any fibres from the gasserian ganglion join the lateralis

nerve cannot be decided. The ophthalmicus profundus-gasserian ganglionic complex is completely separate from the facialis ganglion. A small pre-profundus placode is present on both sides of the head in the fore-brain region. It extends about 60 microns dorso-ventrally by 60 microns antero-posteriorly on one side, and 50 by 70 microns on the other side. The placode is in cellular continuity with the ectoderm but is partly separate from it. Some of the nuclei of the cells are undergoing mitosis (see Pl. 1, fig. 2.).

The lateralis constituent of the facialis ganglion gives off the r. buccalis facialis which lies close to the developing neuromast organs in the skin. The r. superior ophthalmicus facialis emerges from the dorsal surface of the lateralis ganglion. It appears to merge into the ectoderm and cannot be followed very far. Proceeding

Fig. 1.



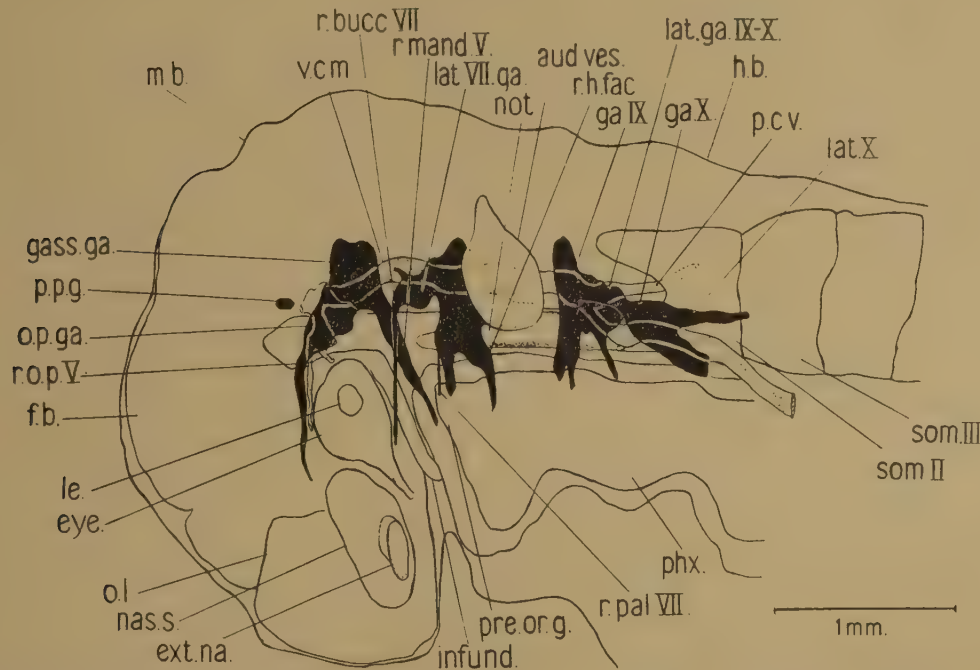
15 mm. stage. Lateral reconstruction showing the relationship of the cranial ganglia to the brain. The metotic somites, their related spinal nerves and the early arteries are recorded. (Key to the references p. 296.)

posteriorly the crest and epibranchial constituents of the facialis ganglion are intimately associated (Pl. 1, fig. 3). This stage is comparable to the older stages of *Amblystoma jeffersonianum* in Landacre's account (1933). No separate acoustic ganglion is distinguishable, though from the posterior region of the facialis ganglion nerve fibres go to the auditory epithelium. The postero-ventral region of the facialis ganglion is connected with a large nerve mass which lies just ventral to the anterior region of the facial musculature. This nerve tissue is probably the r. hyomandibularis facialis. The extremely fine r. palatinus facialis running mesio-ventrally arises from the antero-ventral region of the facialis

ganglion. It is pre-spiracular and innervates the dorsal surface of the mouth (text-figs. 1, 2).

The glossopharyngeal ganglion extends from its insertion as a dorso-ventrally elongated mass approximately 100 microns posterior to the auditory vesicle. On one side the post-auditory lateralis ganglion dorsally connects ganglia IX and X, while on the other side there appears to be crest material also lying ventral to the lateralis constituent. The relation of ganglion IX to the pharyngeal endoderm recalls that of the facialis ganglion. The vagus ganglion has myotome medial to it (text-fig. 1). A vagus branchial nerve I runs to the yolky endoderm of the presumptive second branchial cleft, and the lateralis portion of the ganglion separates from it dorsally as we proceed posteriorly. The ventral posterior mass becomes indistinguishable from the surrounding tissue.

Fig. 2.



15 mm. stage. Lateral reconstruction showing the vena capitis medialis and its relation to the ganglia and other structures. (Key to the references p. 296.)

The metotic somites.

According to Platt (1896 a), the first metotic segment in *Necturus* is the glossopharyngeal, it has no myotome and no ventral root. The myotome of the second metotic segment disappears ventrally but its dorsal portion joins the muscle of the third metotic segment. The third, fourth and succeeding somites develop myotomes. The myotomes of the fourth, fifth and sixth segments grow down ventrally forming the hypoglossal musculature innervated by the ventral roots of the fourth and fifth segments. The sixth segment (third of the trunk) has a complete spinal nerve (ganglion, dorsal and ventral root). Goodrich's (1911)

description of *Amblystoma* agrees with Platt except that he finds a ventral root in segment 3, and a dorsal root in segment 5. In the 15 mm. stage *Cryptobranchus japonicus* spinal nerves I and II (fourth and fifth metotic segments) both have a ganglion with dorsal and ventral roots (Pl. 1, fig. 4). In spinal nerve I the ventral root divides into an upper ramus innervating the mesial surface of the myotome of the fourth metotic segment, and a ventral ramus which runs mesial to this muscle and ends in the lateral plate tissue. In spinal nerve II the dorsal ramus innervates the myotome of the fifth metotic segment and the ventral ramus ends in the lateral plate anterior to the presumptive pronephric tubules (text-fig. 1). No hypoglossal (spino-occipital) nerve (ventral root of third metotic segment) is yet present. It is found in all later stages.

A small ventral muscles lies between the vagus ganglion and notochord (separate from the latter) (text-fig. 1). Though lying close to the posterior myotome of the third metotic segment it can be distinguished from the latter. In the 19 mm. stage it is more intimately fused with the myotome of the third metotic segment and attached to the notochord. It could not be found in the 26 mm. stage. From the material it seems likely that the ventral muscle fibres of the second metotic segment disintegrate and disappear by the 26 mm. stage (Goodrich, 1911; Platt 1896). The innervation of this rudimentary muscle is probably by the hypoglossal nerve when this is present. The myotome of the third metotic segment, including the dorsal portion of the muscle of the second metotic segment at the level of the presumptive condyle region, extends 800 microns antero-posteriorly along the dorsal margin and 300 microns along the ventral margin. It is innervated ultimately by the hypoglossal nerve. In the 15 mm. stage the dorsal portion of the muscle does not reach the auditory vesicle, but in the 19 mm. and later stages it reaches the dorso-posterior surface of the auditory vesicle.

Blood system.

The vena capitis medialis arises just anterior to the eye. It runs posteriorly mesial to the cranial ganglia, close to the mid-brain. It lies mesio-ventral to the lateralis X ganglion and lateral to the ventral border of the myotome of the third metotic segment, leading into a large sinus amongst the yolk cells. At the level of the origin of vagus branchial nerve I it receives a post-cerebral vein which drains blood from the hind-brain region (Pl. 1, fig. 2, text-fig. 2).

The ventral aorta arises from a sac-like heart as a single vessel which runs anteriorly and divides into a bi-lateral pair of vessels (aortic arches II) (Pl. 1, fig. 3). Each vessel curves around the pharynx latero-dorsally; slightly anterior to the origin of the r. palatinus facialis they curve posteriorly. The paired aortic vessels run mesial to the head ganglia to join posteriorly, forming the median dorsal aorta. An internal carotid on each side runs forwards, sending a branch to the infundibulum and then lying mesial to the eye above the optic stalk, ending in the mesenchyme between the fore-brain and ectoderm (text-fig. 1).

(b) The 17 mm. stage larva.

General features.

Differentiation of the tissues of this specimen is much more advanced than that of the 15 mm. specimen and is indeed little different from the 19 mm. stage. This tissue differentiation is noticeable in the origin of the cranial nerves and their branches, muscle delimitation and differentiation, origin of procartilage in the basal plate region, development of more elaborate blood vessels, more compact arrangement and fusion of the various ganglia, origin of gill pouches and the loss of yolk from certain tissues. In the 17 mm. stage there is a straightening-out of the flexure at the anterior end. This reorganization is reflected in the position and arrangement of the eye and optic nerve, nasal sac and r. ophthalmicus profundus V. The latter is nearer a horizontal position instead of lying almost vertically as in the 15 mm. stage (text-fig. 5). Neither mouth nor gill cleft open to the exterior. The spiracular pouch has withdrawn slightly from its position near the epidermis, a condition intermediate between the 15 mm. and 19 mm. stages. Five further endodermal gill pouches occur on each side, these reaching the ventral epidermis of the pharynx.

Cranial nerves.

These will be described in some detail in the 19 mm. stage. Only a few points of interest will be mentioned in this stage.

The trochlear nerve was recognizable on one side only, arising from the ventro-anterior region of the mid-brain above the margin between mid- and fore-brain. It could not be followed along its course. Just behind this nerve and close to the brain is a small round ganglion extending 60 microns antero-posteriorly by 100 microns dorso-ventrally. It is present on one side only. Nerves III and VI were not recognized; they had probably not yet formed.

The r. ophthalmicus profundus V terminates on the latero-anterior surface of the nasal sac. At about the level of the optic lens a ventral branch is given off which lies close to the mesial surface of the eye. An anterior division passes as a fine strand lateral to the nasal sac, while a posterior division runs slightly posteriorly just dorsal to the nasal sac, ventro-mesial to the eye. This branching nerve may be the deep profundus V which later in development anastomoses with the truncus infraorbitalis. No other branches were recognized. The r. maxillaris V is separate from the r. buccalis facialis throughout its length. They join at their ventral ends at the latero-posterior surface of the nasal sac (text-fig 5).

The r. hyomandibularis facialis is in general the same as in the 19 mm. stage but less complex.

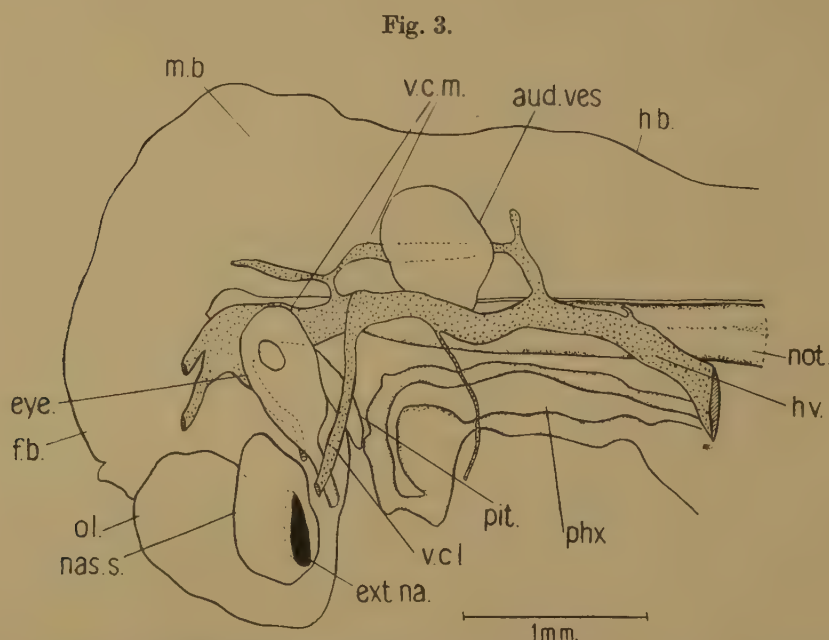
Nerve IX is similar to that in the 19 mm. stage. A small dorsal nerve probably of lateralis fibres is given off dorsal to nerve IX and vagus branchial nerve I on both sides of the head. There is a single r. lateralis X running posteriorly along each side of the body. A hypoglossal (spino-occipital) nerve, and spinal nerves I and II are well developed. Spinal nerves I and II differ from those in the 19 mm. stage by being smaller, less well developed, and spinal nerve I is separate from

the truncus intestino-accessorius X. The first and second spinal nerves are separate from one another. Spinal nerve I has a rudimentary ganglion and no dorsal root, whereas spinal nerve II has a well-developed ganglion and a dorsal root (text-fig. 5).

Blood system.

The venous system.

The vena capitis medialis is reduced in the region mesial to the auditory sac; it has completely disappeared here in the 19 mm. stage. The anterior portion of the vena capitis medialis is retained mesial to the trigeminus ganglion and the r. ophthalmicus profundus V. In general the venous system is similar to that of the 19 mm. specimen (see text-figs. 3, 7). In the 17 mm. specimen, however, a posteriorly directed vein arises just behind the junction of the vena capitis lateralis with the vena capitis medialis. It lies close to the skin, lateral to the r. mentalis internus facialis and jugularis facialis, and ventro-lateral to the facial musculature.



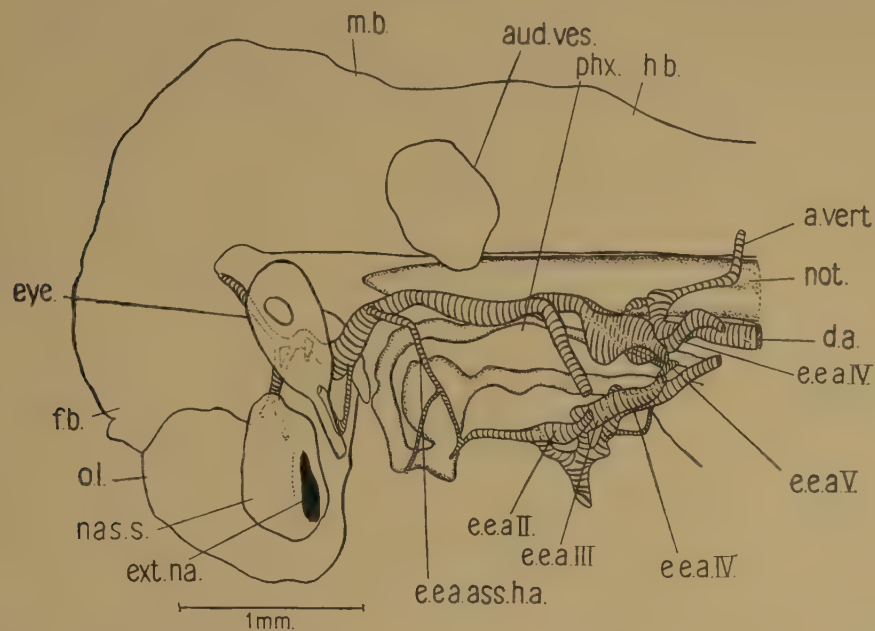
17 mm. stage. Lateral reconstruction showing the venous system. (Key to the references p. 296.)

The arterial system.

Leading from the sac-like heart a median truncus arteriosus divides into five pairs of aortic arches which join the main lateral aortae dorsally (text-fig. 4). The efferent epibranchial artery I (aortic arch II) is later associated with the hyoid arch. Efferent arteries II, III and IV (aortic arches III, IV and V) are the vascular loops associated with the external gill filaments. The efferent epibranchial artery V (aortic arch VI) is complete, but since the lungs have yet to be formed, no backwardly directed vessel which ultimately becomes the pulmonary artery is

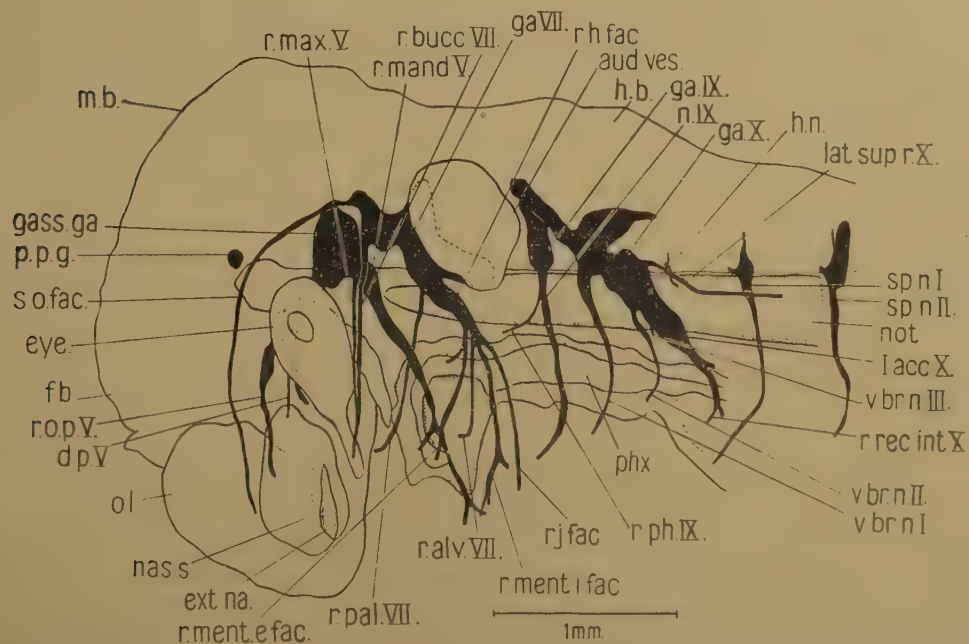
developed. The lateral dorsal aortae join to form the median dorsal aorta 200 microns behind spinal nerve I. Leading from the efferent epibranchial artery I is a small ventro-anteriorly directed vessel. It lies lateral to the r. mandibularis V.

Fig. 4.



17 mm. stage. Lateral reconstruction showing the arrangement of the arteries. (Key to the references p. 296.)

Fig. 5.



17 mm. stage. Lateral reconstruction showing the arrangement of the cranial ganglia, peripheral and anterior spinal nerves. (Key to the references p. 296.)

The lateral dorsal aortae continue anteriorly as the internal carotid arteries. Approximately 100 microns anterior to the efferent epibranchial artery I a ventro-mesial vessel is given off. It lies close to the infundibulum and is distributed to the ventro-mesial surface of the eye (supra orbital artery). The internal carotids supply blood to the ventro-lateral surface of the fore-brain; inclining dorsally they meet in a medial plexus on the ventral surface of the fore-brain. Behind the efferent epibranchial arteries a vertebral artery arises from the lateral dorsal aorta. It has a paired origin, becoming a single posteriorly running vessel lying mesial to the musculature of that region and close to the notochord. It leads to the spinal cord posterior to the origin of spinal nerve I (text-fig. 4).

(c) The 19 mm. stage larva.

General features.

Aoyoma (1930) found the first signs of cartilage at the 19.5 mm. stage. In his 20 mm. stage he describes a rudimentary formation of a basal plate, short trabeculae cranii, Meckel's cartilage, hyoids, four pairs of branchial arches and otic capsules. In my 19 mm. stage the trabeculae cranii and basal plate are recognizable as concentrations of rounded or elongated nuclei surrounded by a dense fibrous matrix. The basal plate is especially reminiscent of hyaline cartilage (Pl. 1, fig. 7). Meckel's cartilage and the hyobranchial regions show aggregations of chondroblasts with large rounded nuclei closely packed together and little cytoplasm. The trabeculae cranii lie almost vertically, joining behind with the short basal plate. The latter is slightly keel-shaped at its ventral surface, extending antero-posteriorly for about 700 microns (text-figs. 6, 8). The notochord ends at the anterior edge of the basal plate (crista sellaris) and runs through the basal plate as a cylindrical rod. No otic capsules are recognizable. Internal to the r. mandibularis V and vena capitis lateralis, and external to the vena capitis medialis and internal carotid, a faint suggestion of the delimiting of the pterygo-quadrangle cartilage is seen (Pl. 1, fig. 7).

Cranial Nerves.

The olfactory nerve I arises from the lateral margin of the olfactory lobe (olfactorius glomerulus), and leads posteriorly as a solid mass of fibres to the nasal sac. Here it divides into several branches which are distributed to the nasal epithelium.

The optic nerve II appears from the ventral surface of the fore-brain running outwards and slightly upwards to the eye. It has a diameter of 60 microns and is hollow in part. It lies ventral to the r. ophthalmicus profundus V.

The trochlear nerve IV is inserted in the antero-ventral region of the mid-brain. It runs posteriorly along the ventro-lateral region of the mid-brain lying dorso-mesial to the anterior edge of the eye and mesial to the vena capitis medialis. It then dips down to innervate the superior oblique muscle. Its total length is approximately 600 microns from its insertion to the muscle (text-fig. 6).

The abducens nerve VI emerges from the ventro-lateral region of the mid-brain at the level where the anterior basicapsular commissure will eventually form, and where the r. hyomandibularis facialis is separating off from the facial ganglion (text-figs. 6, 8). It runs ventrally for a short distance and some fibres appear to join the facial ganglion about 15 to 20 microns posterior to the origin of the r. palatinus facialis. They could not be followed further. The rest of the nerve runs anteriorly mesial to the r. palatinus facialis, but its later course could not be determined.

The trigeminus nerve V. The trigeminus ganglion is situated lateral to the mid-brain and mesial to the primordium of the pterygo-quadratus. It is about 300 microns long antero-posteriorly and of variable width, up to 400 microns at its widest part (Pl. 1, figs. 6, 7; text-fig. 6).

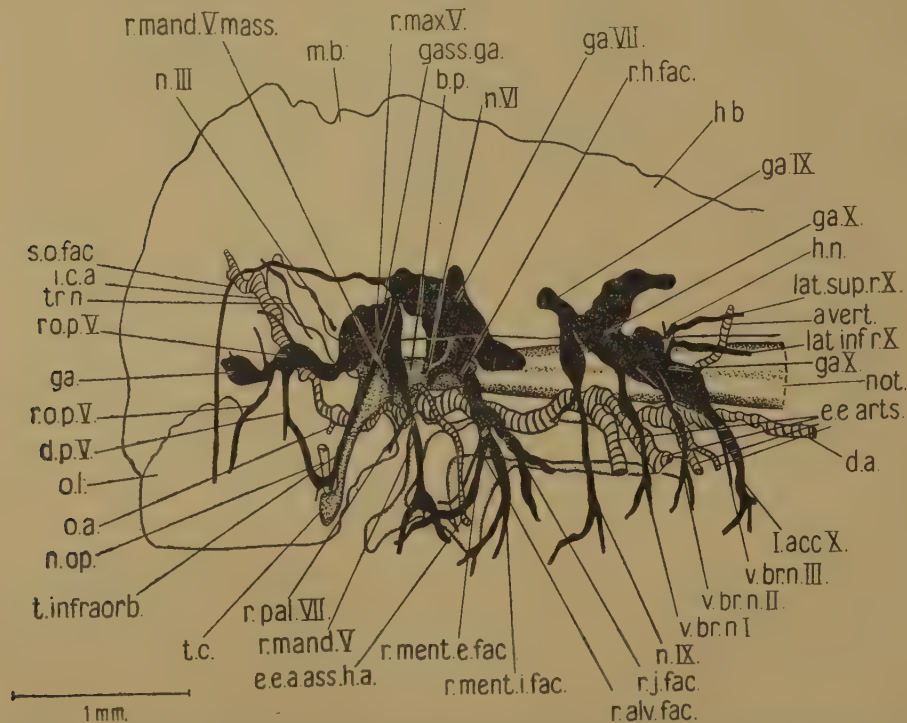
(a) The r. ophthalmicus profundus V runs forwards mesial to the eye, at first lying lateral to the vena capitis medialis, then dorsal to the optic nerve and ventral to the vena capitis medialis close to the inner surface of the eye. It gives off a deep profundus V branch to the truncus infraorbitalis, this branch lying mesial and close to the eye in its downward path. Two small dorsal branches are given off as the main nerve pursues its course anteriorly, but no palatine profundus branch was recognized. The main nerve then lies mesio-ventral to the inner anterior edge of the eye above the posterior edge of the nasal sac (text-figs. 6, 8). Here it gives rise (on both sides) to a lower branch lying over the nasal sac while an upper branch appears to lead into a ganglion. This ganglion is 250 microns long antero-posteriorly on one side and 130 microns long on the other side (Pl. 1, fig. 5). Leading from the ganglion (on each side) is a delicate nerve running dorso-laterally in the direction of the ectoderm.

We thus find that in the 15 mm. stage there is a small epidermal placode part at least separate from the epidermis and lying on both sides of the head in the fore mid-brain region. In our 17 mm. stage there is, on one side only, a small ganglion attached to the brain just behind the trochlear nerve, and in the 19 mm. stage there is the ganglion just mentioned, found anterior to the trigeminus ganglion on each side of the head. Owing to shortage of material this feature could not be investigated in more detail. Little would be gained by commenting on these results.

(b) The gasserian ganglion gives off a slender branch which lies close to, though it is distinguishable from the r. buccalis facialis (Pl. 1, fig. 6). A fine branch from the outer r. buccalis facialis leads to the skin and another fine nerve runs ventrally lateral to the vena capitis lateralis. This nerve innervates the skin in the maxillary region and is doubtless the r. maxillaris V proper. The compound rami buccalis VII and maxillaris V (truncus infraorbitalis) runs ventro-lateral to the eye fairly close to the skin (text-fig. 7). It branches in a complex manner beneath the optic nerve. An outer branch leads to the skin, an inner branch appears to end over the posterior region of the nasal sac, while a middle branch proceeds anteriorly underneath the eye and receives the deep profundus V. The junction of the truncus and the deep profundus V is ventral to the anterior eye region and here a fine branch runs to the skin lateral to the nasal sac. The truncus infraorbitalis ends ventral to the anterior region of the eye lateral to the nasal sac.

(c) The r. mandibularis V arises from the posterior end of the gasserian ganglion posterior to the origin of the r. maxillaris V, and runs lateral to the primordium of the pterygo-quadratus (Pl. 1, fig. 7). At the level where the r. mandibularis V arises the r. superior ophthalmicus facialis and the r. buccalis facialis unite dorsally, this junction being the anterior margin of the facialis ganglion (Pl. 1, fig. 7; text-figs. 6, 7). The latter is separate from the gasserian ganglion, though in the later stages ganglia V and VII are fused together forming a trigemino-facialis complex. The r. mandibularis V runs ventro-laterally and posteriorly through the masseter muscle. It sends a fine branch to join the r. mentalis externus facialis on one side only, while the rest of the nerve leads postero-laterally and ventrally close to the region of the future Meckel's cartilage. It forks into an anterior division which curves forwards, running ventral to the lower jaw, and a posterior division leading to the skin of the lower jaw on the ventral surface. At the origin of the r. mandibularis V a branch is distributed to the masseter muscle (text-figs. 6, 7).

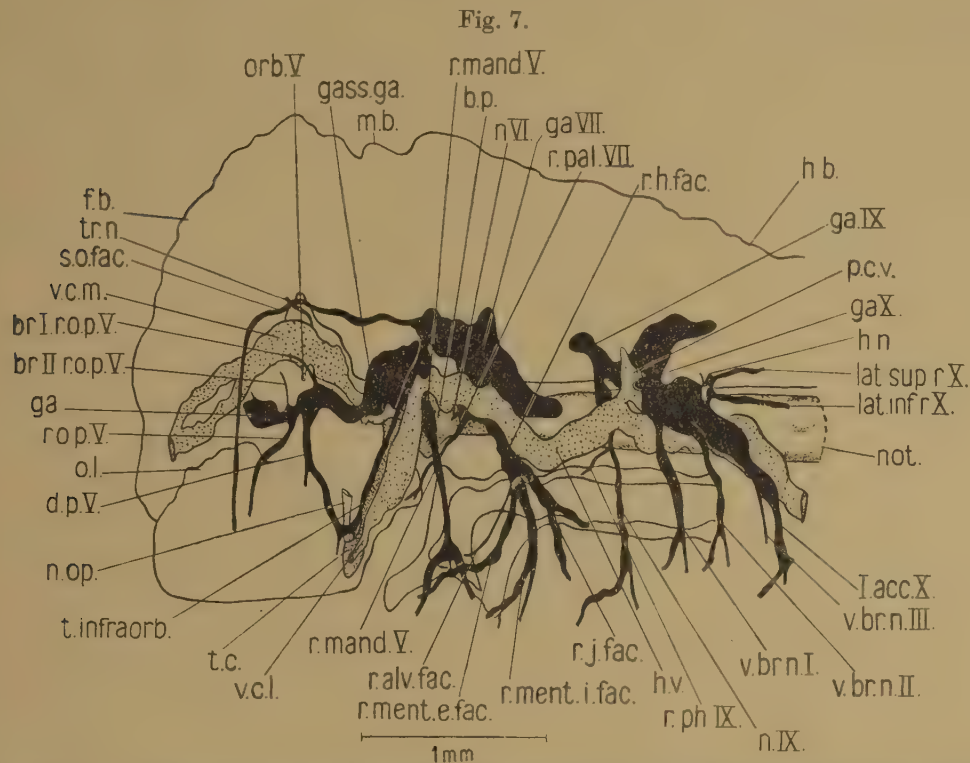
Fig. 6.



19 mm. stage. Lateral reconstruction showing the relationship of the cranial nerves and ganglia to the arteries and early cartilage. (Key to the references p. 296.)

The facialis nerve VII. (a) The r. buccalis facialis runs ventro-anteriorly for about 90 microns and then receives fibres from the trigeminus ganglion. The truncus infraorbitalis has been described, the lateralis constituent innervating the neuromasts of the skin along its course.

(b) The r. superior ophthalmicus facialis arises from the antero-superior end of the facialis ganglion (lateralis constituent) dorsal to the origin of the r. buccalis facialis. It runs forwards antero-laterally close to the skin, innervating the dorsal neuromasts, lying dorsal but close to the eye. Proceeding anteriorly, it lies near the skin approximately two-thirds of the way up the side of the head lateral to the vena capitis lateralis, and finally dips downwards, ending on the ventral surface of the snout lateral to the termination of the r. ophthalmicus profundus V. It is completely separate from the latter (Pl. 1, fig. 5; text-figs. 6, 7).



19 mm. stage. Lateral reconstruction showing the relationship of the cranial nerves and ganglia to the veins and early cartilage. (Key to the references p. 296.)

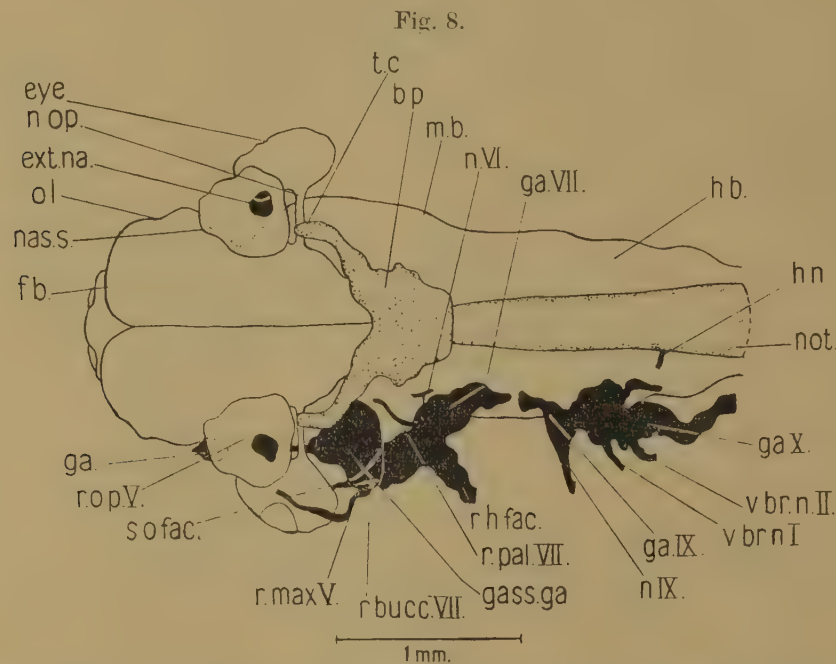
(c) The r. hyomandibularis facialis separates off from the postero-ventral region of the facialis ganglion (Pl. 1, fig. 8). It runs posteriorly for approximately 150 microns and then curves forwards dividing into three branches.

(i) The r. mandibularis internus facialis (r. alveolaris facialis) runs ventrally as a delicate strand mesial to the region of the future Meckel's cartilage. It lies close to the wall of the tympanic pouch, continuing forwards until it merges in the nuclear mass in this region. It lies mesial both in origin and distribution to the r. mandibularis externus facialis and mesial to the efferent epibranchial artery 1 (text-figs. 6, 7).

(ii) The r. mandibularis externus facialis divides into an anterior r. mentalis externus facialis, which runs antero-laterally to the region of the future Meckel's

cartilage and is associated with the lateral line organs. The posterior r. mentalis internus facialis curves slightly posteriorly, dividing into two branches which innervate the skin of the lower jaw (text-fig. 6).

(iii) The r. jugularis facialis runs postero-laterally for about 200 microns (text-fig. 6). An antero-ventral branch runs alongside the rudiment of the hyoid arch, curving round underneath it to innervate the M. ceratohyoideus externus and the M. intermandibularis posterior, while a posterior branch runs for a short distance horizontally external to the muscles in the vicinity near the body wall. There is no VII-IX (Connection of Willis) joining the r. jugularis facialis to the glossopharyngeal nerve.



19 mm. stage. Ventral reconstruction showing the brain and early cartilage, and the relationship of the cranial ganglia to the latter and other head structures. (Key to the references p. 296.)

The glossopharyngeal nerve IX. Ganglion IX, joined to ganglion X by a narrow bridge, is fairly short antero-posteriorly and elongated dorso-ventrally. Nerve IX has a fine ventral r. pharyngeus IX which runs anteriorly close to the lateral dorsal aorta and then underneath the latter to innervate the roof of the pharynx, and a large r. post-trematicus IX which runs horizontally and slightly ventro-posteriorly to lie behind gill pouch I. It curves anteriorly to innervate the future M. ceratohyoideus internus, and it also probably innervates the M. ceratohyoideus externus.

The vagus nerve X. The vagus branchial nerve I arises from ganglion X about 200 microns behind the origin of nerve IX (Pl. 1, fig. 9; text-fig. 6). It lies behind gill pouch II, turning anteriorly and forking. A r. pharyngeus is probably present. Vagus branchial nerve II arises 120 microns posterior to the preceding nerve and lies behind gill pouch III; it also forks. A small r. pharyngeus is probably

present. Vagus branchial nerve III arises just anterior to the truncus intestino-accessorius X. It lies behind gill pouch IV. There are three lateralis nerves, a ramus lateralis superior, inferior, and ventralis. The rami laterales superiores and inferiores arise at the same level as the hypoglossal nerve and run posteriorly. The superior ramus lies closer to the side of the body than the inferior ramus. The slender r. lateralis ventralis X runs postero-ventrally lateral to spinal nerve I and close to the body wall. The truncus intestino-accessorius X leads postero-ventrally, sending two gastric branches to the gut, a cardiac branch to the heart, and an anterior r. recurrens intestinalis branch lying between the gut and the heart (text-fig. 24).

Just anterior to the vagus branchial nerve I a delicate dorsal nerve arises from ganglion X and appears to be distributed to the skin. Whether it is a cutaneous or lateralis nerve cannot be ascertained.

The *hypoglossal (spino-occipital) nerve* arises from the ventro-lateral region of the hind-brain (Pl. 1, fig. 10). It divides into an upper ramus innervating the upper mesial surface of the muscle of the third metotic segment, and a lower ramus which innervates the ventro-mesial region of this muscle.

Blood system.

Anteriorly the vena capitis medialis resulting from the union of two vessels lies dorso-mesial and then mesial to the eye. It runs backwards dorsal then mesial and ventral to the r. ophthalmicus profundus V, receiving a pituitary vein before joining the vena capitis lateralis. It lies mesial to the primordium of the pterygo-quadrates, ventral to the trigeminus ganglion, and after joining the vena capitis lateralis below the anterior edge of the facialis ganglion the resulting head vein proceeds posteriorly ventro-lateral to the latter. It continues lateral to the r. hyomandibularis facialis, ventral to the auditory sac, internal to the M. digastricus and just latero-dorsal to the lateral dorsal aorta. It continues lateral to nerve IX, receiving here the post cerebral vein, then mesial to the branchial nerves, lying ventral and then mesial to the vagus ganglion. It lies over the truncus intestino-accessorius X underneath the lateralis X nerves as it leads to the heart (text-fig. 7).

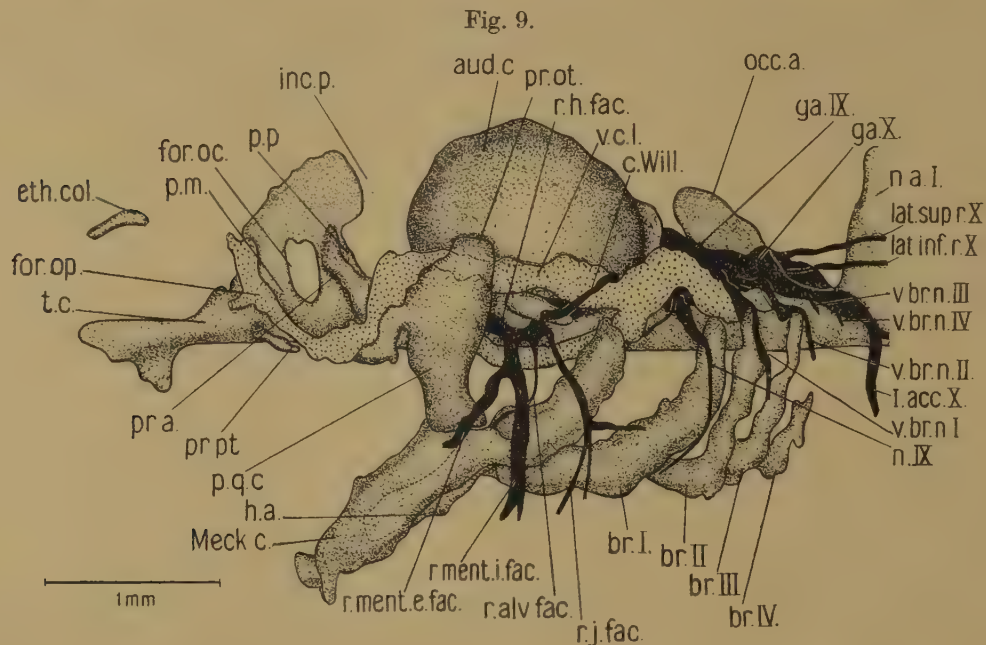
The vena capitis lateralis runs from the posterior nasal sac region posteriorly ventral to the eye and truncus infraorbitalis. It continues lateral to the gasserian ganglion and r. mandibularis V and finally joins the vena capitis medialis.

The general pattern of the arterial system is similar to that in the 17 mm. stage. The relationship of the arteries to the nerves, etc. can be seen from text-fig. 6.

(d) The chondrocranium and ossifications in the 26 mm. and 30 mm. stage larvae.

In the 26 and 30 mm. stages there are a well-developed chondrocranium and hyobranchial skeleton, some early ossifications, four functional gill clefts which open to the exterior, and a mouth opening. Kawagoe (1932) reported open gill clefts by the 23 mm. stage. The 19 mm. stage has no internal nares, but in the 26 mm. stage there are internal and external nares with a choanal canal leading from the mouth to the exterior. Internal nares were reported in *Cryptobranchus japonicus* (26.5 mm.) by Murayama (1928) and Miyawaki (1929), and in the

28.0 mm. stage by Aoyama (1928). In the 26 mm. stage the chondrocranium is about 4.0 mm. long (text-fig. 9) and in the 30 mm. stage it is 4.5 mm. long (text-fig. 14). The trabeculae cranii are 1.7 mm. long in the former and 2.5 mm. long in the latter. From the ventral view they appear as curved rods lying fairly close to each other anteriorly but diverging as one proceeds posteriorly (text-figs. 10, 16). The trabeculae are wide apart ("platytrabic"). This condition may be secondary, as in the early *Stegocephalia* they lie near together (Watson, 1926; De Beer 1937). In the 30 mm. stage at the mesio-anterior end of the nasal sac the trabecula becomes elongated dorso-ventrally and convex (convexity facing inwards) to enclose the anterior end of the nasal sac (text-fig. 14). A ventro-lateral outgrowth (solum nasi) lies underneath the anterior nasal sac region. The development of the nasal capsule in urodeles including *Cryptobranchus alleghaniensis* has been

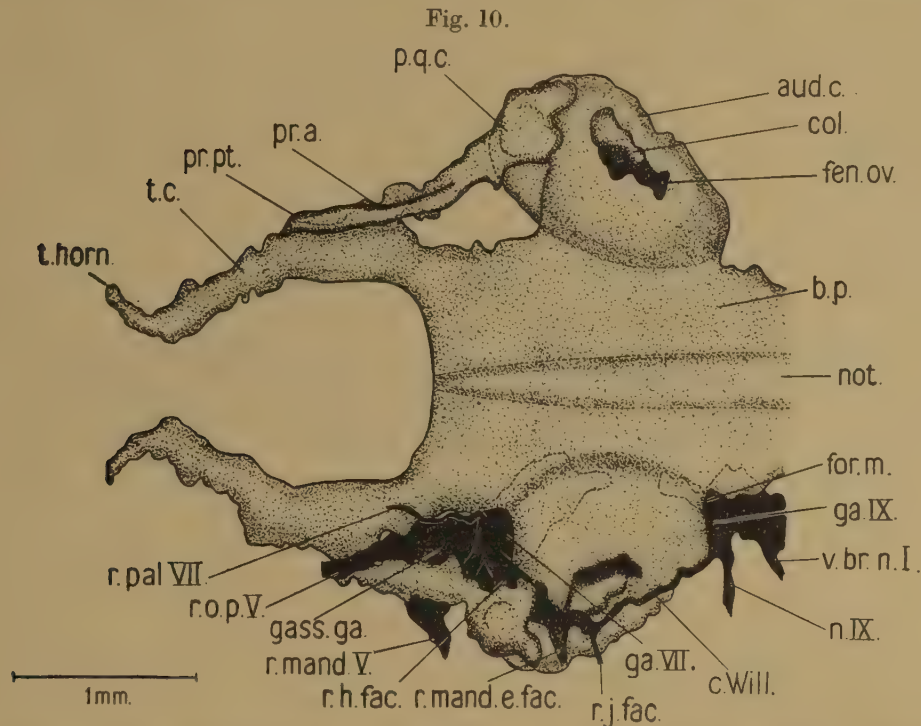


26 mm. stage. Lateral reconstruction of the chondrocranium, Meckel's cartilage and hyobranchial skeleton, with part of the related venous system and cranial nerves. (Key to the references p. 296.)

described by Higgins (1920). There is no lamina antorbitalis. The anterior edge of the basal plate (crista sellaris) lies behind the pituitary; and the plate continues posteriorly, merging into the floor of the occipital arch. The large space anterior to the crista sellaris and bounded laterally by the trabeculae cranii is the future foramen hypophyseos. The anterior end of the notochord lies just behind the pituitary. It bulges slightly from the ventral surface of the basal plate though always enclosed by cartilage.

The pre-occipital and occipital arches arise behind the auditory capsule, the border between the arches being defined by a single slit-like hypoglossal foramen. In *Amblystoma* (Goodrich 1911) the pre-occipital arch arises in the septum between the first and second myotomes (second and third metotic segments), the first

metotic segment having disappeared. The occipital arch arises in the septum between the second and third myotomes (third and fourth metotic segments). There is no evidence of the disappearance of segments behind the vagus described by Fürbringer (1897), and thus there is no objection to the view that the hind end of the skull may shift backwards or forwards in the course of phylogeny. Goodrich supposes that the ancestors of the Amphibia had three occipital segments only. Fürbringer (1897), Osawa (1902), and Aoyama (1930) describe a hypoglossal nerve emerging via the hypoglossal foramen in *Cryptobranchus*, and this is confirmed by the present work. Goodrich (1911) described a ventral nerve root to the third metotic segment in the Axolotl, but it is lost during later development.



26 mm. stage. Ventral reconstruction of the chondrocranium with related ganglia. Fenestra ovalis and columella are clearly demonstrated. The processus pterygoideus is omitted on one side. (Key to the references p. 296.)

There is no roof at all to the chondrocranium. The fissura metotica has a cartilaginous upper margin by the 30 mm. stage.

No cranio-vertebral joint was recognizable.

The side wall of the chondrocranium is better developed in the 30 mm. than in the 26 mm. stage, especially in front of the foramen optica. But it is generally similar. The taenia marginalis posterior (commissura orbito-parietalis) has developed little further, however, and there is no dorsal boundary to the incisura prootica. Between the foramen oculomotorius and the incisura prootica (on one side only) in the 30 mm. stage is a small foramen which transmits the hypophysial vein (the "pituitary vein" of some authors: Goodrich 1930, p. 272).

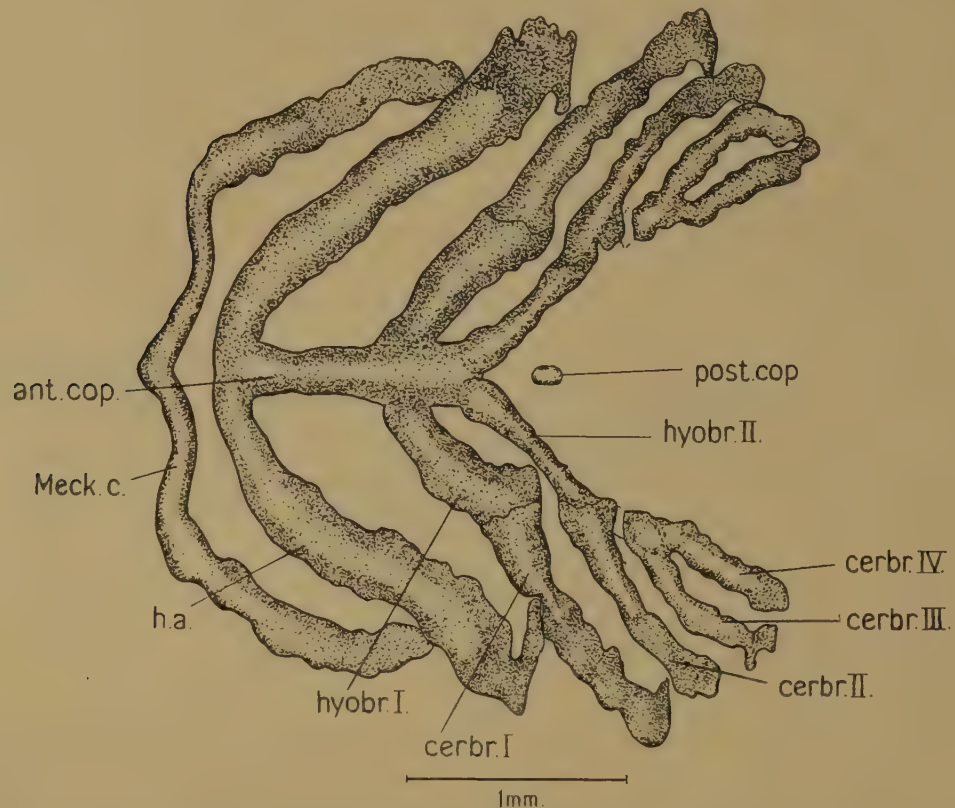
Reed, 1909). During phylogeny the facial nerve has slipped off the end of the stylus, partially in perennibranchiates and completely in caducibranchiates (De Beer, 1937, p. 461).

The 26 mm. stage has no post-palatine process separating the hyomandibular and palatine nerves. In the 30 mm. stage this is slightly developed on one side. In *Necturus* these nerves do not traverse the auditory capsule but pass between it and the lateral margin of the parachordal plate (Terry, 1919). In *Amblystoma* these nerves appear to emerge from the auditory capsule cavity, but they are completely separated from it by the capsule wall. This condition is primitive and important, since the condition in other urodeles (where the capsule wall is not chondrified and the facial nerve seems to pass through the capsule) and in Anura can be derived from it (De Beer 1937, p. 178). In the 30 mm. stage *Cryptobranchus* the palatine nerve emerges from the skull via its own foramen in the lateral region of the basal plate (Pl. 2, fig. 8). The hyomandibular nerve lies between the lateral margin of the basal plate and the mesial wall of the auditory capsule. The antero-mesial wall of the latter is perforated by the fenestra acoustica (Stadtmüller, 1924, *Salamandra*; Miyawaki 1929, Aoyama 1930, *Cryptobranchus japonicus*), and it is here that the hyomandibular separates from the facialis ganglion. The presence of this fenestra gives the impression that the hyomandibular nerve traverses the auditory capsule cavity, because there is no mesial wall to the latter. Behind the fenestra acoustica is the smaller fenestra perilymphatica. The fenestra endolymphatica lies dorsal to and in between the two lower fenestrae. It is the largest of the three and extends dorso-ventrally (text-fig. 17). Hay (1890) and Kingsley (1892, 1902a) in the larval *Amphiuma*, and Platt (1896a) in a 46 mm. *Necturus* described a dorsal fenestra endolymphatica, and three lower foramina on the auditory capsule medial wall. *Salamandra* has three fenestrae early in development though more are present later (Stadtmüller 1924), while Miyawaki (1929) in an 80 mm. stage *Cryptobranchus japonicus* found a dorsal fenestra endolymphatica, a fenestra acoustica anterior, medius and posterior, and a fenestra perilymphatica.

The pterygo-quadrate lies lateral to the chondrocranium and has three processes joining it to the latter. The processus pterygoideus is present at the 28 mm. stage (Aoyama 1930). It is present by my 26 mm. stage. In the latter the anterior end fuses on one side with the trabecula; behind there is a separate nodule of cartilage; the remainder is merely a continuation of the pterygo-quadrate. It is complete on the other side (text-fig. 11). This suggests that the processus pterygoideus is at least in part probably formed as an independent chondrification *in situ*. In the 37 mm. stage of *Cryptobranchus* Edgeworth (1923 a) describes a chondrified processus pterygoideus having its anterior end confluent with the trabecula and the inner surface of the antorbital process. Edgeworth (1925) suggests that the ancestral urodele condition is one in which the processus pterygoideus is continued anteriorly and joins the trabecula. In *Amblystoma*, *Desmognathus*, *Spelerpes*, *Salamandrella*, and *Ranodon*, the anterior portion of the process does not develop beyond the condition of a cellular strand. In *Ranodon*, however, the palato-quadrate persists throughout its anterior extent and is connected with the ethmoidal region in the adults (Jarvik 1942). The reduction

of the processus pterygoideus in the former examples is probably secondary (Edgeworth 1925), *Cryptobranchus japonicus* has a complete cartilage bar (as have *Hynobius* and *C. alleghaniensis* Edgeworth 1925, Jarvik 1942), with an ethmoid attachment to the trabecula, and is primitive in this respect. During later larval life in *Cryptobranchus japonicus* the anterior part of the palato-quadrato bar is completely resorbed (Jarvik, 1942). The palato-quadrato in urodeles may have two different connections with the ethmoid region,

Fig. 12.



26 mm. stage. Ventral reconstruction of Meckel's cartilage and the hyobranchial skeleton.
(Key to the references p. 296.)

a medial larval one and a lateral definitive one, probably corresponding exactly to the connections in anurans formed by the commissura quadrato-cranialis anterior and the processus quadrato-ethmoidalis respectively. Normally the palato-quadrato in urodeles is much reduced anteriorly, and with the exception of *Ranodon* has undergone regression (Jarvik, 1942).

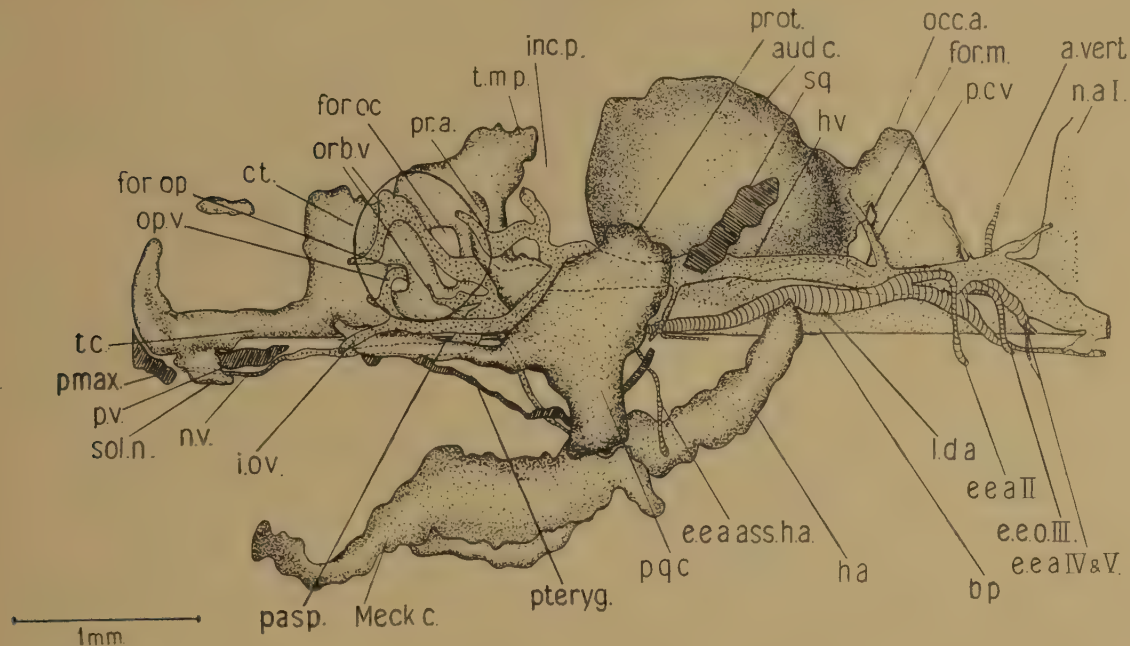
In the 32 mm. stage of *Cryptobranchus japonicus* a rudimentary processus basitrabecularis arises as a small finger-like process from the lateral edge of the basal plate.

The processus ascendens and oticus are normal and require no comment: for their morphological relations, see the illustrations and De Beer (1926, 1937). In urodeles the ascending process fuses with the pila prootica before the otic or basal processes have fused with the neurocranium. In *Ceratodus* the basal process fuses first, then the otic and lastly the ascending process (Allis, 1914).

Meckel's cartilage is about 2.4 mm. long (26 mm. stage); slightly longer in the 30 mm. stage. From its median anterior symphysis (with its fellow from the other side) it runs postero-laterally and articulates with the mesial surface of the base of the pterygo-quadrato.

The hyobranchial skeleton in the 26 and 30 mm. stages differs in size (text-figs. 11, 12, 14). The hyoid shows no division into ceratohyale and hypohyale (agrees with Aoyama 1930, and Fukuda 1928). Branchiale I and II show a faintly marked

Fig. 13.



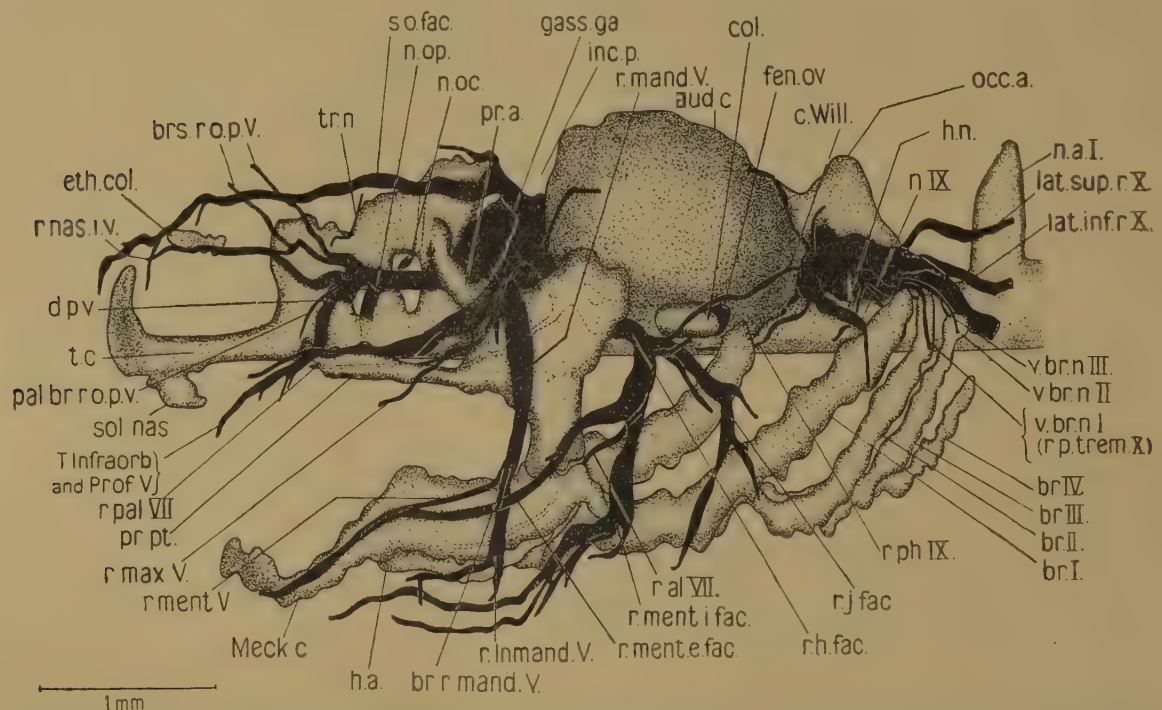
30 mm. stage. Lateral reconstruction of the chondrocranium, Meckel's cartilage and the hyoid arch, with the venous system, post-ptyergo-quadrato arterial system and ossifications associated with the cartilage structures. Part of the squamosal has been omitted. (Key to the references p. 296.)

division into ceratobranchiale and hypobranchiale and in the 30 mm. stage ceratobranchiale III and IV are in cartilaginous connection with ceratobranchiale II on each side. (This agrees with Fukuda's (1928) description of his 30 mm. larva.) About 0.2 mm. posterior to the anterior copula is an isolated nodule of cartilage 0.15 mm. long (post copula) (text-fig. 12). Edgeworth (1920) suggests that in *Menopoma* this cartilage was originally a ventro-posterior process of the second basibranchial which separates off and subsequently chondrifies. Aoyama (1930) and Fukuda (1928) suggest that it is formed *in situ* as an isolated cartilage. There is no branchial plate, which is common in larval salamandrids, but entirely absent in *Necturus*, *Siren lacertina* and *Cryptobranchus* (L. Smith 1920).

Osteocranium development.

The premaxilla, squamosal, and dentary (all paired), and median parasphenoid are beginning to form in the 26 mm. stage. The dentary and premaxilla were reported in the 28 mm. stage by Aoyama (1930). In the 30 mm. stage the premaxillae are separate irregularly shaped bones about 260 microns long lying just anterior to the solum nasi (text-figs. 15, 16). Two separate teeth rudiments lie mesial to the premaxilla. The r. nasalis internus profundus V runs mesial to the nasal sac and then lies below the premaxilla, innervating the skin of the anterior snout region. The prevomer is about 500 microns long lying posterior to the premaxilla and ventral to the solum nasi (Pl. 2, fig. 7; text-figs. 15, 16).

Fig. 14.



30 mm. stage. Lateral reconstruction showing the relationship of the cranial ganglia and peripheral nerves to the cartilage structures. (Key to the references p. 296.)

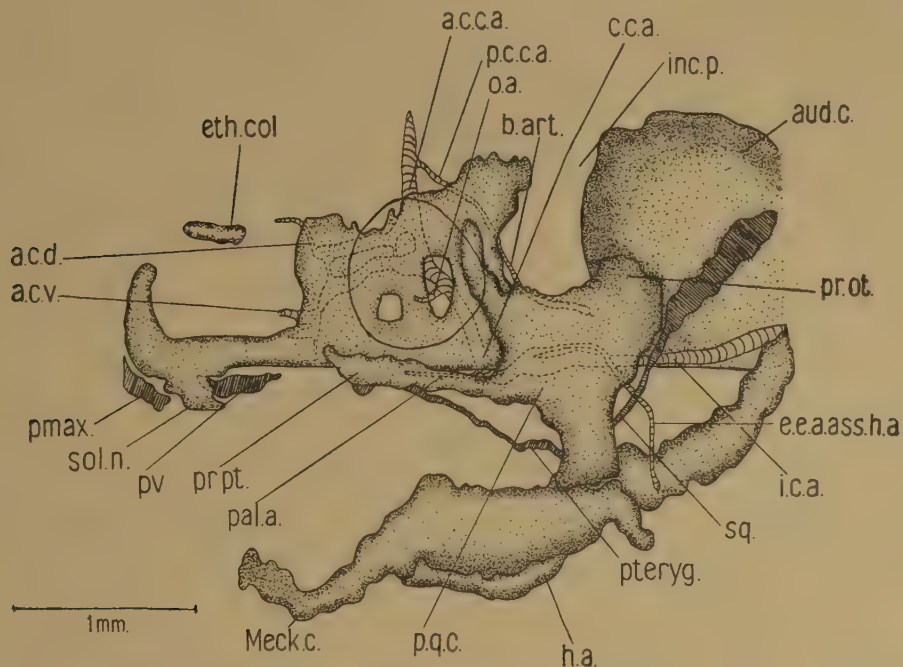
Teeth rudiments lie ventral and ventro-lateral to this ossification and later become attached to it (De Beer 1937). The pterygoid is a thin elongated spindle lying underneath the processus pterygoideus and extending to the articular region of the pterygo-quadrate. It is toothless as in *Triton* and *Amblystoma* (De Beer 1937). The palatine bone does not appear to be present at this stage.

The squamosal arises as a vertical strut lateral to the pterygo-quadrate and columella (Thyng 1906). Later its dorsal end grows into a plate flanking the auditory capsule (text-figs. 15, 16).

The parasphenoid is a thin lamella lying below the brain between the ventral edges of the trabeculae. Its anterior and posterior edges are ill-defined though it seems to end posteriorly near the anterior edge of the basal plate (text-fig. 16).

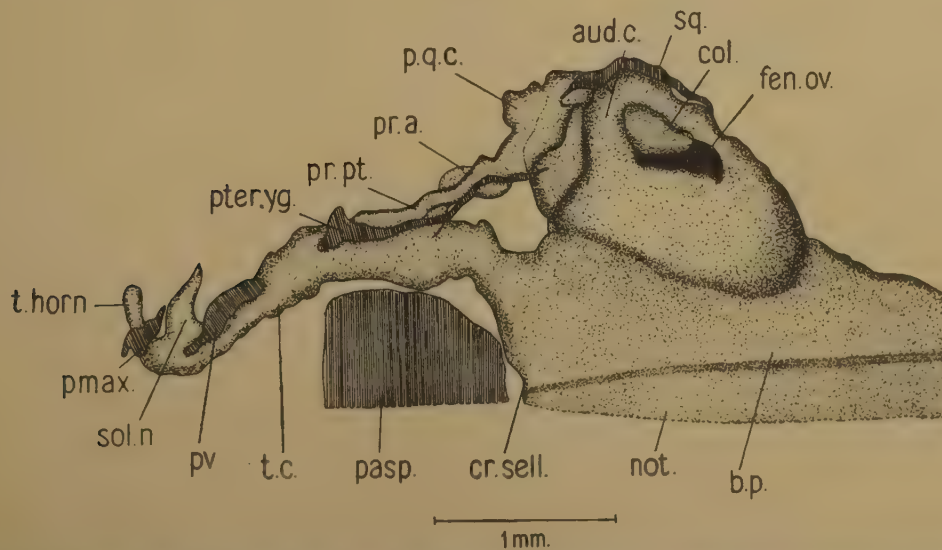
The dentary lies ventro-lateral to Meckel's cartilage, extending for approximately 1.8 mm. It is separated from its fellow at the median symphysis by a nodule of cartilage. Eight teeth rudiments lie dorsal and separate from the dentary on each side. Fusion with teeth follows at the 35 mm. stage (Aoyama 1930).

Fig. 15.



30 mm. stage. Lateral reconstruction of part of the chondrocranium, Meckel's cartilage and the hyoid arch with the related anterior arterial vessels. Some of the ossifications are included. (Key to the references p. 296.)

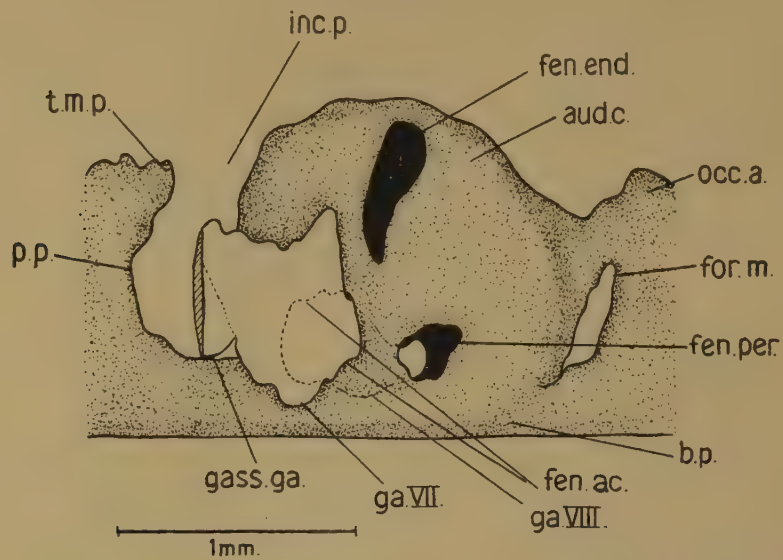
Fig. 16.



30 mm. stage. Ventral reconstruction (one side only) of the chondrocranium and related ossifications. (Key to the references p. 296.)

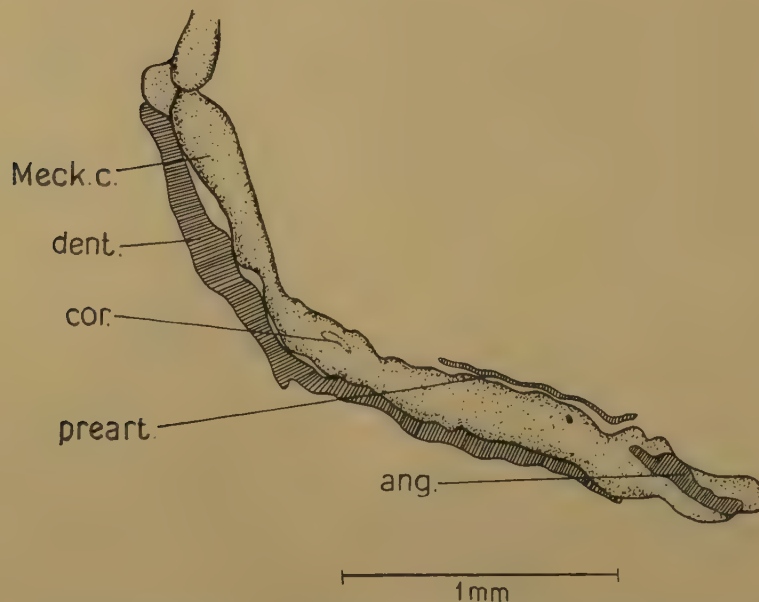
The prearticular (goniale) lies on the ventro-mesial side of Meckel's cartilage in the posterior region. It is a flattened lamella 0.75 mm. long. The angular

Fig. 17.



30 mm. stage. Medial view of the auditory capsule showing the medial fenestrae and the related facialis and acoustic ganglia. (Key to the references p. 296.)

Fig. 18.



30 mm. stage. Ventral reconstruction of Meckel's cartilage and related ossifications. (Key to the references p. 296.)

about 0.4 mm. long lies in the ventro-posterior region of Meckel's cartilage. It has vague boundaries (text-fig. 18). The angular is present in *Ranodon sibiricus*, *Salamandra keyserlingi*, and *Hynobius nebulosa* (Stadtmüller 1937). There is

no sign of a supra-angular (absent in recent Amphibia, Gregory 1913), or an articular (unossified in recent Amphibia, Gregory 1913).

All the bones described except the angular were reported by Aoyama (1930) in his 31 mm. stage *Cryptobranchus japonicus*.

Situated 0.32 mm. anterior to the prearticular on the inner upper surface of Meckel's cartilage is a spindle of bone 100 microns long and present on both sides of the head. This ossification is probably the coronoid. In addition to these ossifications the 32 mm. stage possesses a pair of thin flattened bones arising dorsal to the nasal capsule (nasals) and a posterior pair lying above the taenia marginalis posterior and the auditory capsule (parietals) (text-fig. 19). The trochlear nerve is distinct from the latter.

(e) The cranial and anterior spinal nerves and blood vessels in the 30 mm. stage.

Nervous system.

The olfactory nerve I has a double origin, an antero-lateral root and a posterior ventral root. The posterior ventral root is distributed to the antero-mesial surface of the nasal epithelium. The antero-dorsal root lies ventral to the ethmoid column and on proceeding posteriorly lies ventral to the r. nasalis internus profundus V and mesial to the posterior nasal epithelium (Pl. 2, fig. 7).

Kingsley (1892) described the olfactorius as arising by a single root in *Amphiuma*, but in 1902 he considered the origin to be paired. Norris (1908) agrees with Kingsley. Kingsbury (1895) and Fish (1895) described the origin as by a single root in *Necturus*. Earlier, Gage (1893) in *Diemyctylus*, and Lee (1893) in *Spelerpes* and *Salamandrina* had described a double origin to the olfactorius; so did McGregor (1896) in *Cryptobranchus alleghaniensis*, for he stated that within the cranium the olfactory nerve had the appearance of being double. Similarly Coghill (1902, 1906) in *Amblystoma* and *Triton*, Terry (1906) in *Amblystoma*, Dodds (1906) in *Plethodon*, and Norris (1910, 1913) in *Siren*, noted the double origin of this nerve. Norris & Buckley (1911) state that the double origin is more evident in the adult *Necturus* and *Spelerpes*, and in my specimens the two groups of fibres are clearer at the 30 mm. stage than in the 26 mm. and 19 mm. stages.

The oculomotor nerve III emerges from the mid-brain at the level of the top of the crista trabecula (Pl. 2, fig. 2). This origin from the floor of the mesencephalon is general among the urodeles. From its insertion it leads ventro-anteriorly to emerge via the foramen oculomotorius. It divides into a superior and inferior ramus. In the 32 mm. stage on one side a delicate nerve joins the profundus nerve to nerve III where the latter divides into upper and lower rami. The r. oculomotorius superior is distributed to the rectus superior, the r. oculomotorius inferior is distributed to the recti inferior, and internus (anterior), and the inferior obliquus. The nerve has a diameter of 40 microns.

Osawa (1902) in the adult *Cryptobranchus japonicus* described its course to the usual eye muscles; a r. ciliaris is said to lead to the eye. Furthermore the oculomotor nerve may anastomose with the trigeminus nerve as in *Amblystoma* (Coghill, 1902), and *Salamandra* (Francis 1934). *Triton* is similar to *Amblystoma* but variable (Coghill 1906), while *Amphiuma* (Norris 1908) is variable in arrangement also. Dodds (1906) in *Plethodon* described the innervation of the eye muscles by the oculomotorius;

he described a few fibres which go to the eye-ball. The eye muscle nerves are imperfectly developed in *Siren* (Norris 1910, 1913) and *Necturus* (Norris & Buckley 1911). McKibben (1913) described the arrangement and distribution of the oculomotorius in *Necturus* in detail.

The trochlear nerve IV was more satisfactorily analysed in the 32 mm. stage, to which the present description relates. Nerve IV emerges from the brain approximately dorsal to the foramen optica and runs anteriorly and mesial, separate from but close to branch I of the r. ophthalmicus profundus V, at the level of the upper edge of the crista trabecula. It lies almost over the head vein in this region. It then runs over branch II of the profundus, lying lateral to the latter, and finally innervates the superior obliquus, entering it on the dorso-mesial surface.

Osawa (1902) in the adult *Cryptobranchus japonicus* records its origin over the oculomotorius and its distribution to the superior obliquus. In *Necturus*, Kingsbury (1903) found its origin in the brain, while McKibben (1913), after describing its origin from the caudal border of the dorsal surface of the mid-brain, noted that it sometimes anastomoses with the profundus nerve. Norris (1908), investigating *Amphiuma* specimens ranging from 55 mm. to 300 mm. notes its mid-brain origin. He found the nerve composed of only two to three fibres and Herrick (1914) found it composed of merely ten fibres. Gage (1893), in the adult *Diemyctylus*, states that the nerve emerges via a separate foramen, and that in the larva it emerges with the oculomotorius by a common foramen. It is considered the smallest nerve in *Amblystoma* (Herrick 1894), being composed of only thirty fibres. It leaves the skull through a foramen in the parietal bone and associates with the profundus on its way to the superior obliquus. Coghill (1902) agrees with Herrick but finds no anastomosis between nerve IV and the profundus. In *Triton* these nerves may or may not exchange fibres (Coghill 1906).

In general in the urodeles the delicate trochlearis nerve arises from the dorsal region of the mid-brain, usually associates with a branch of the r. ophthalmicus profundus V and is distributed to the superior obliquus. In addition to the genera mentioned, the general statement applies also to *Siren* (Norris 1913), *Spelerpes* (Bowers 1900), and *Salamandra* (Francis 1934).

The abducens nerve VI arises from the ventro-lateral surface of the mid-brain just mesial to the facialis ganglion. It emerges by an extremely fine slit-like foramen abducentis, and on emerging ventral to the basal plate separates into two.

In *Necturus* Kingsbury (1895) found the origin of nerve VI caudal of nerve VII from the ventral floor of the metencephalon. McKibben (1913) agrees with Kingsbury's results; the former found only ten to fifteen fibres in this nerve. It runs anteriorly, ventral to the gasserian ganglion (there being no exchange of fibres), to the rectus externus. Norris (1908) in *Amphiuma* found nerve VI arising by two roots slightly posterior to nerve VII; it innervates the rectus externus. It arises from the ventral aspect, midway between nerves VIII and IX in *Desmognathus* (Fish 1895), and caudal to nerve VIII in *Diemyctylus* (Gage 1893), and *Plethodon* (Dodds 1906). Its diameter in the latter genus is 65 microns. It has a similar origin in *Triturus torosus* (Smith 1927).

In *Amblystoma* (Herrick 1894; Coghill 1902) and *Triton* (Coghill 1906) the abducens nerve arises from the ventral surface of the medulla under the origin of nerve IX. It innervates the rectus externus and possibly the retractor bulbi (Herrick) and the levator bulbi (Coghill). In *Spelerpes* nerve VI arises at the level of the most anterior roots of the IX-X nerves. It divides into two roots and innervates the rectus externus and the retractor bulbi (Bowers 1900). In *Cryptobranchus alleganiensis* it appears to have an origin similar to that of *Spelerpes* (McGregor 1896), while in *Cryptobranchus japonicus* Osawa (1902) reports nerve VI originating from the medulla to innervate the rectus externus. It arises by two roots from the ventral surface of the medulla posterior to the IX-X complex in *Salamandra* (Francis 1934, Goodrich 1930, p. 248). The nerve has its own foramen in the basal plate "im vorderen Teil der Basal platte medial von dem Facialis austitt" (Gaupp 1911 a).

To sum up: The abducens nerve of urodeles arises from the ventral surface of the medulla in the region of nerve roots VII-IX. The nerve runs anteriorly below the trigeminus ganglion and the r. ophthalmicus profundus V to innervate the rectus externus and perhaps the retractor (and levator?) bulbus muscles. It is generally believed to be present though very small in the Amphibia (Fish, 1895).

The trigeminus nerve V. (a) *The r. ophthalmicus profundus V* is merely a continuation of the trigeminus ganglion running horizontally forwards, mesial to the processus ascendens and over the optic nerve (Pl. 2, fig. 3). The arrangement is complex and is probably variable in different specimens. On one side of the present specimen the main r. ophthalmicus profundus V splits into two and then subsequently unites (text-fig. 14). This reconstituted nerve is the r. nasalis internus profundus V. Just after dividing branch I is given off (homologue of the profundus minor in *Siren*, Wilder, 1891; Norris, 1913). Branch I runs antero-dorsally mesial to the r. superior ophthalmicus facialis to the skin of the dorso-lateral region. Farther forward, arising from the upper division of the r. ophthalmicus profundus V is another branch, which has a similar distribution to branch I. The rejoined r. nasalis internus profundus V (the junction is 350 microns anterior to the origin of the deep profundus V) runs anteriorly, dorso-mesial to the nasal sac, underneath the ethmoidal column and over the olfactory nerve (Pl. 2, fig. 7). It ends ventral to the premaxilla and innervates the skin. The deep profundus V runs vertically from its place of origin at the level of the origin of branch I. It divides into two branches and these join the truncus infraorbitalis. The resulting nerves are distributed to the skin and sense organs lateral to the nasal sac (text-fig. 14).

The palatine profundus V is a delicate strand lying mesial to the deep profundus V. It runs close to the side wall of the chondrocranium, eventually lying mesial to the posterior end of the nasal sac. The nerve was followed to the region where the r. palatinus facialis ends, these nerves lying very close together, if not yet anastomosing (text-fig. 14).

Norris (1913) describes the arrangement and distribution of the r. ophthalmicus profundus V in *Siren*. After giving off the r. ophthalmicus profundus minor (Wilder 1891) the main branch divides into three. This is a general feature in urodeles, having been described by many investigators in different genera, i.e. *Plethodon* (Dodds 1906, Norris 1909), *Amblystoma* (Herrick 1894, Coghill 1901, 1902), *Necturus* (Norris 1911, Norris & Buckley 1911), *Spelerpes* (Bowers 1900, Norris 1911), *Siren* (Norris 1910, 1913), *Triton* (Coghill 1906), *Amphiuma* (Wilder 1892, Norris 1908), *Salamandra* (Francis 1934), and *Cryptobranchus japonicus* (Osawa 1902).

These three branches are as follows. The r. nasalis internus V which leads to the mesial surface of the nasal sac over the olfactory nerve. It gives off a dorsal branch to the skin in the antero-dorsal snout region, and then divides into nervi ophthalmici anteriores (Wilder, 1891) which innervate the side of the snout. The r. nasalis externus V runs antero-laterally round the anterior wall of the eye-ball, and then divides into three or four branches which enter the capsule along the inner border of its lateral wing. The third branch is the palatine profundus V, which anastomoses with the r. palatinus facialis. This profundus-palatine

anastomosis is general among the urodeles (Kingsley, 1896, 1902 b). It is reported in *Cryptobranchus alleghaniensis* (Wilder 1892, McGregor 1896), and *Cryptobranchus japonicus* (Osawa 1902). According to Norris in *Siren* the palatine profundus V and the r. palatinus facialis both divide into two which unite in pairs in such a way that the nerves both contain profundus and palatine elements. One of these nerves runs lateral and the other mesial to the nasal epithelium. *Siren* also shows a profundus-truncus infraorbital anastomosis which modifies the general plan, and this is further complicated by the fact that the r. palatinus facialis divides into a lateral and mesial branch shortly after leaving the geniculate ganglion. In the 30 mm. larva of *Cryptobranchus japonicus* we can homologize certain nerves with those of *Siren*. Branch I has been accounted for. The split rami are together the r. nasalis internus profundus V. The separation is curious since it does not happen on the other side in this specimen, nor in any of the other stages. It is an example of the variability of the urodele cranial nervous system to which Coghill (1902, 1906) and McKibben (1913) have alluded. The r. nasalis internus V gives off a dorsal branch in both *Siren* and *Cryptobranchus japonicus*. The palatine profundus V is easily compared in these animals, though in the 19 mm. larva of *Cryptobranchus japonicus* it was not yet recognizable.

An anastomosis between the deep profundus V and the truncus infraorbitalis is present in my 19 mm. and older stages. This condition is not uncommon in urodeles (Norris 1913). In *Amphiuma* (Norris 1908) the r. buccalis facialis joins with two branches of the r. ophthalmicus profundus V. The condition is similar in *Cryptobranchus alleghaniensis* (Wilder 1892) and *japonicus* (Osawa 1902).

It appears that in the 30 mm. stage larva of *Cryptobranchus japonicus* there is no free r. nasalis externus profundus V because it has anastomosed with the truncus infraorbitalis. The final position of this nerve, however, is lateral to the nasal sac in a position similar to where the r. nasalis externus profundus V would normally be. Thus the deep profundus V (or part of it) is the homologue of the r. nasalis externus profundus V. This anastomosis is not present in *Amblystoma*, *Triton* (Coghill 1902, 1906) or *Salamandra* (Francis 1934). It is not mentioned by Bowers (1900) in *Spelerpes* or by Dodds (1906) in *Plethodon*.

(b) The r. mandibularis V arises posterior to the r. maxillaris V, just anterior to the level of fusion of the r. superior ophthalmicus facialis and r. buccalis facialis, and runs lateral to the pterygo-quadrate (Pl. 2, fig. 4; text-fig. 14). It gives off a branch to the masseter muscle (this branch is generally present in urodeles), and the main r. mandibularis V then divides into a (i) r. mentalis V, (ii) r. intermandibularis V, (iii) branch to the r. mentalis externus facialis, (iv) branch to the r. alveolaris facialis.

The r. mentalis V, r. intermandibularis V, and the branch to the r. mentalis externus facialis arise at the same place (text-fig. 14). The r. mentalis V runs anteriorly, mesial to the branch to the facial nerve and lateral but close to Meckel's cartilage. It first lies mesial but gradually becomes dorso-lateral to the dentary on continuing anteriorly, touching the r. mentalis externus facialis. The two nerves are almost a single compound nerve. The latter proceeds to the symphysis of the lower jaw. In the urodeles generally the r. mentalis V runs along the

dorso-lateral aspect of the dentary as the anterior fork of the r. mandibularis V. It enters a canal in the dentary in *Cryptobranchus alleghaniensis* (McGregor 1896, Wilder 1892), *Amphiuma* (Kingsley 1902 a, Norris 1908), *Salamandra* (Francis 1934), and *Amblystoma* (Herrick 1894, Coghill 1902). The nerve runs lateral to the lower jaw and does not enter a canal in the dentary in *Siren* (Wilder 1891, Norris 1913). A branch of the r. mentalis V enters the dentary in *Necturus* (Norris & Buckley 1911), while the main branch runs along the side of the jaw giving off branches to the skin. *Spelerpes* is similar to *Necturus* (Norris 1911), though Bowers (1900) did not mention the internal branch. The internal branch in *Necturus* emerges from the dentary near the anterior end and supplies the skin. A small branch is given off which associates with the r. alveolaris VII (Norris & Buckley 1911).

The r. intermandibularis V runs vertically between Meckel's cartilage and the lateral dentary. It runs antero-ventral to Meckel's cartilage, innervating the M. intermandibularis posterior. There is a small posterior division in the 32 mm. stage. The r. intermandibularis V is a general feature in the urodeles. According to Norris in *Siren* (1913) it contains motor and cutaneous components.

The r. mandibularis V has a small branch which anastomoses with the r. mentalis externus facialis, the resulting compound nerve running along the antero-lateral surface of the lower jaw latero-dorsal to the dentary. It is similar in the 26 mm. specimen. The alveolar branch of the r. mandibularis V is difficult to follow. Its junction with the r. alveolaris facialis is not recognizable, at least at this early stage.

The alveolar V branch is present in many urodeles, i.e. *Amblystoma* (Herrick 1894, Coghill 1902), *Triton* (Coghill 1906), *Plethodon* (Norris 1909), *Salamandra* (Francis 1934), *Necturus* (Norris & Buckley 1911) and *Cryptobranchus japonicus* (Osawa 1902). It was not reported by Bowers (1900) in *Spelerpes*, Wilder (1891) in *Siren*, and Kingsley (1902 a) in *Amphiuma*, but Norris (1908, 1911, 1913) recorded the nerve in these animals respectively.

(c) *The r. maxillaris V* fibres from the gasserian ganglion run both mesial to and over the r. buccalis facialis, but more fibres lie mesial and finally ventral to the latter. The ventral r. maxillaris V soon receives some of the dorsal trigeminal fibres which pass lateral to the truncus infraorbitalis and join the r. maxillaris V. The latter continues anteriorly ventro-lateral to the truncus infraorbitalis and close to the skin in the maxillary region of the upper jaw (text-fig. 14). It is generally similar in the 26 mm. stage (text-fig. 11). The weak development and slight forward extent of the r. maxillaris V are characteristic of the urodeles. This condition plus the strong development of the profundus differ considerably from elasmobranchs, brachiopterygia (*Polypterus*), actinopterygians, Dipnoi, and Anura (Jarvik 1942).

The facialis nerve VII. (a) *The r. superior ophthalmicus facialis (truncus supraorbitalis)* nerve has been called the r. frontalis (Herrick 1894) and the r. nasalis (Osawa 1902). It has been reported in *Amblystoma*, *Triton*, *Amphiuma*, *Necturus*, *Spelerpes*, *Siren*, *Menopoma* and *Cryptobranchus japonicus*, etc. It innervates the supraorbital neuromast system (Norris 1913), and it is not found in terrestrial forms where the lateralis nerves are lost during ontogeny, e.g. *Plethodon*

(Norris 1909). In the larvae of *Cryptobranchus japonicus* it is distributed to the lateral line organs along the dorso-lateral surface; it lies over the anterior tip of the nasal sac and ends on the ventral tip of the snout (Pl. 2, figs. 1, 2, 3, 7; text-figs. 11, 14). There is no anastomosis between the r. superior ophthalmicus facialis and the dorsal branches of the r. ophthalmicus profundus V; however, Norris (1910) in *Siren* finds general cutaneous fibres from the gasserian ganglion in the supraorbital trunk.

(b) *The r. buccalis facialis.* In my larval specimens this nerve emerges ventro-anteriorly from the anterior end of the facialis ganglion. It receives cutaneous fibres from the gasserian ganglion and the composite nerve then runs lateral to the temporalis muscle, just dorsal to the r. maxillaris V and ventral to the eye. The truncus infraorbitalis (r. buccalis and its trigeminus constituent (Pl. 2, figs. 2, 3; text-figs. 11, 14) has been found in all larval urodeles that have been investigated. Goodrich (1930) writes, "the r. buccalis facialis is closely associated with the r. maxillaris V". The truncus continues anteriorly, giving off cutaneous and lateralis fibres to the skin. Postero-ventral to the eye it divides into an outer division which leads to the skin (or neuromasts), while an inner division subsequently branches in a complex manner. At the level where it receives the deep profundus V it has already divided in three branches. The two outer divisions anastomose with the two divisions of the deep profundus V while the inner branch runs antero-mesially to the anterior end of the processus pterygoideus; mesial to the posterior end of the nasal sac towards the termination of the r. palatinus facialis. In *Triton* the truncus infraorbitalis reaches the cephalic border of the eye and here the r. maxillaris V enters the maxilla leading to the upper lip; the r. buccalis facialis lying mesial sends a filament medially, which penetrates the cartilaginous wall of the nasal capsule, and passing round the caudal border of the nasal epithelium and the internal nares joins the mesial branch of the ophthalmico-palatine nerve (Coghill 1906). Norris (1913) in *Siren* describes a branch of the truncus containing buccalis VII and maxillaris V fibres, forming an anastomosis with the fibres of the r. ophthalmicus profundus V of the palatine profundus anastomosis. The branch passes into the nasal capsule ventral to the r. nasalis internus V, and after giving off its general cutaneous constituent supplies the infraorbital series of neuromasts at the sides of the tip of the snout. In *Cryptobranchus alleghaniensis* a branch from the r. maxillaris superior runs across the floor of the nasal capsule to join the r. ophthalmicus profundus V, and the r. maxillaris superior is clearly associated with the r. buccalis facialis (McGregor 1896).

In my material the nerve running mesially from the truncus infraorbitalis is recorded in the 26, 30 and 32 mm. stages on both sides, so there is no doubt of its presence.

(c) *The r. palatinus facialis* nerve arises from the antero-ventral region of the facialis ganglion (geniculate constituent), in front of the post-palatine commissure, which separates it from the r. hyomandibularis facialis. It emerges from the brain through a foramen in the ventro-lateral region of the basal plate and lies just over the lateral dorsal aorta and mesial to the pterygo-quadrangle (Pl. 2, figs. 5, 8;

text-figs. 11, 14). It continues anteriorly ventro-lateral to the basal plate and trabecula, innervating the roof of the pharynx. Fibres from the palatal plexus enter the palatal (vomarine teeth) in *Amblystoma tigrinum* (Herrick 1924). At the anterior end of the processus pterygoideus the r. palatinus facialis divides into two delicate branches. It lies mesial to the post-nasal sac and no division lateral to the internal naris is recognizable. A lateral palatine branch (in addition to a mesial branch) is described by Coghill (1901) in *Amblystoma* and *Rana*, and by Norris (1913) in *Siren*. Osawa (1902) in the adult *Cryptobranchus japonicus* reports a small lateral division ending near the post-choanal opening. The r. palatinus facialis associates with the branch running mesially from the truncus infraorbitalis in the region postero-mesial to the nasal sac, though the details of the r. palatinus facialis, palatine profundus V, and the truncus infraorbitalis branch cannot be analysed in this material.

No palatine caudalis (post-palatine of Wilder 1891) was recognizable in any of my larvae. Nor was it found in the adult *Cryptobranchus japonicus* (Osawa 1902) and *alleghaniensis* (McGregor 1896). A true Jacobson's anastomosis (post-palatine caudalis and r. pharyngeus IX) is present in *Amphiuma* (Norris 1908), *Amblystoma* (Herrick 1894, Coghill 1902), *Triton* (Coghill 1906), *Siren* (Norris 1910, 1913) and *Plethodon* (Norris 1909). There is a diffuse anastomosis in *Necturus*, a few twigs of the palatine caudalis joining with those of nerve IX (Norris 1911).

(d) *The r. hyomandibularis facialis*. (1) *The r. mandibularis internus facialis* (*r. alveolaris facialis*) originates mesio-posterior to the r. mandibularis externus facialis and slightly anterior to the r. jugularis facialis (Pl. 2, fig. 9; text-figs. 11, 14). It leads antero-ventrally mesial to Meckel's cartilage between the latter and the prearticular (Gaupp 1911 b in urodeles generally, De Beer 1937 in *Triton*). According to Norris (1913) there are two features to consider. (1) the nerve divides into two or more branches and one branch enters a canal in the lower jaw; (2) the nerve anastomoses in the canal with the r. mandibularis V.

In the adult *Siren* the r. alveolaris VII passes along the inner border of the goniale (prearticular) and divides into a smaller dorsal and a large ventral branch. It lies between the opercular and Meckel's cartilage although the bone does not enclose the nerve in a canal. It is joined by a branch from the r. mandibularis V, these either fusing or remaining in contact (Norris 1913). The r. alveolaris facialis does not enter a bony canal in *Proteus* and *Necturus* (Kingsbury 1903). Norris & Buckley (1911) in *Necturus* describe the r. alveolaris facialis dividing into two on reaching the lower jaw; there is no anastomosis between this nerve and the r. mandibularis V branch, they merely ramify. In *Amblystoma* (Herrick 1894, Coghill 1902), *Triton*, which is similar to *Amblystoma* (Coghill 1906), *Spelerpes* (Norris 1911), *Amphiuma* (Norris 1908), *Plethodon* (Norris (1909) which is like the larval *Spelerpes*, *Salamandra* (Francis 1934), and *Cryptobranchus japonicus* (Osawa 1902), the r. alveolaris facialis enters a canal in the lower jaw and anastomoses with a branch of r. mandibularis V. In some cases all the r. alveolaris facialis enters the lower jaw, e.g. *Amblystoma*, in other cases only part enters the lower jaw. Norris (1913) sums up: *Proteus*, *Necturus*, and *Siren*, are explained as due to the imperfect development of the opercular bone, this being too rudimentary to form a canal. Nerves V and VII do not fuse completely. The condition in *Proteus*, *Necturus*, and *Siren*, is not primitive but (he goes on to cite Boas) "Das *Siren*, *Menobanchus*, und *Proteus*, Larvenformen seien".

(II) *The r. mandibularis externus facialis* divides into two branches (Pl. 2, fig. 6; text-figs. 11, 14). The r. mentalis externus facialis runs ventral to the squamosal, curving anteriorly lateral to the pterygo-quadrata and Meckel's cartilage. It is

closely associated with the lateral line organs of the lower jaw (Pl. 2, fig. 8). It fuses with a branch of the r. mandibularis V and the composite nerve runs alongside the lower jaw to the median symphysis. The nerve is a constant feature in the urodeles.

The r. mentalis internus facialis is the posterior division, running antero-ventrally to the ventro-mesial region of Meckel's cartilage and subsequently dividing into two (Pl. 2, fig. 4; text-figs. 11, 14). One division lies ventro-mesial to the other. Both divisions lie below the M. intermandibularis posterior and innervate the lateral line organs, though in the 32 mm. stage they appear to innervate the muscle also. These results agree with those reported by other workers on the urodeles.

(III) *The r. jugularis facialis* arises ventral to the place where the r. hyomandibularis facialis receives the Connective of Willis (text-fig. 14). It runs posteriorly in the lateral region of the M. digastricus, the anterior fork innervating the M. digastricus and M. intermandibularis posterior, while the posterior fork seems to innervate the M. ceratohyoideus externus. At the origin of the r. jugularis facialis two nerves arise which lead horizontally to the skin and these proceed posteriorly for a short distance. The upper nerve is associated with the lateral line organs, the lower nerve lies on the lateral surface of the M. digastricus and may be distributed to it. The r. jugularis facialis is a constant feature in the urodeles. A survey of the literature suggests that the nerve innervates the M. digastricus and M. intermandibularis posterior and that it sends cutaneous fibres to the skin. It contains cutaneous and motor components (Norris 1913).

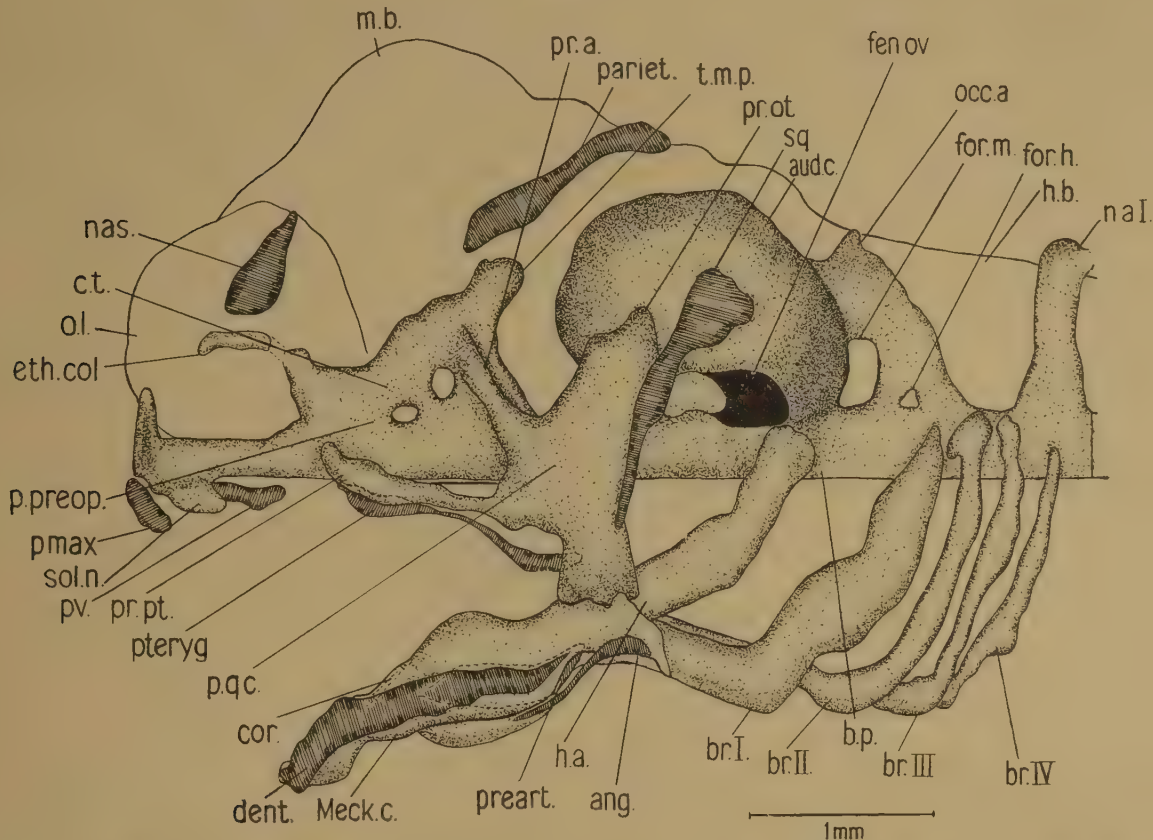
(e) *The lateral line anastomoses with X.* In *Siren* a nerve arises from the dorsal lateral line ganglion just posterior to the origin of the r. superior ophthalmicus facialis, and runs dorso-posteriorly through the masseter, lying beneath the skin. It anastomoses with the r. supratemporalis et auricularis. The latter fibres emerge dorso-posterior to the exist of the r. post-trematicus IX and innervate the neuromasts of the occipital series (Norris 1913).

In the 19 mm. stage of *Cryptobranchus japonicus* just posterior to the junction of the r. superior ophthalmicus facialis and the r. buccalis facialis a delicate nerve arises from the facial ganglion. It leads to the skin, but whether it innervates the neuromasts cannot be ascertained. It is absent in the 17 mm. stage. Just antero-dorsal to the origin of nerve IX another fine nerve arises and leads to the skin. This nerve is present in the 17 mm. stage. There is no continuity between the anterior and posterior nerves.

In the 26 mm. stage two fine nerves arise from the facialis ganglion. They run together as one nerve posteriorly around the anterior margin of the auditory capsule, but cannot be traced very far. They appear to associate with the lateral line organs lying at the level of the junction of the processus oticus with the auditory capsule. Just anterior to the origin of nerve IX two nerves originate from the dorso-lateral margin of the IX-X ganglion. They join and lead anteriorly over the dorso-lateral surface of the auditory capsule closely associated with the lateral line organs. These two nerves may be the r. supratemporalis et auricularis. No connection between the anterior and posterior nerves was seen. The 30 mm. stage is generally the same as in the 26 mm. stage except that the former appears to have a posterior fork to the r. supratemporalis et auricularis (Pl. 2, fig. 8;

text-fig. 14). The 32 mm. stage shows a distinct anterior r. auricularis and 20–30 microns posterior to it a r. supratemporalis, the latter innervating the neuromasts of the occipital region. These nerves lie very close together along their course. It has been suggested by Johnson (1905) in *Petromyzon* that the anastomosing branch of the seventh nerve with its neuromasts might represent the r. oticus in fishes. Norris finds this plausible.

Fig. 19.



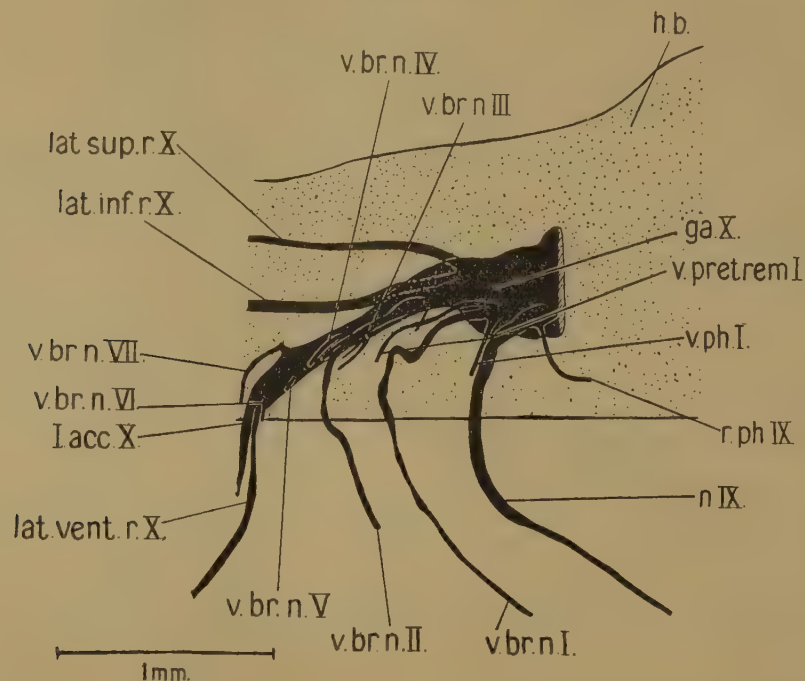
32 mm. stage. Lateral reconstruction of the chondrocranium, Meckel's cartilage and hyobranchial skeleton, and their relation to the brain and ossifications. (Key to the references p. 296.)

In *Siren* and *Amphiuma* the r. supratemporalis and r. auricularis are fused together. The r. supratemporalis was noted by Kingsley (1902 a) and Norris (1908) in *Amphiuma* innervating the occipital sense organs, and Norris (1908) also finds a cutaneous component which corresponds to the r. auricularis vagi. In *Necturus* (Norris & Buckley 1911) and *Spelerpes* (Norris 1911) these two nerves are distinct. Bowers (1900) in *Spelerpes* described both the r. supratemporalis and the r. auricularis; the former innervates the sense organs posterior to the ear, the latter leaves the ganglion in company with the r. supratemporalis and is homologous with Strong's r. cutaneous dorsalis in the Frog. The two nerves are distinct in *Amblystoma* (Coghill 1902) and *Triton* (Coghill 1906), though Coghill thinks they are lateralis nerves only. McGregor (1896) in *Cryptobranchus alleghaniensis* described several branches which innervate the occipital lateral line sense organs; these are probably the rami supratemporalis and auricularis. Osawa (1902) records a r. cutanei in *Cryptobranchus japonicus* arising in the same region.

(f) *The VII-IX Connective of Willis* is similar in the 26, 30 and 32 mm. stages. It arises from ganglion IX, runs round the posterior surface of the auditory capsule and leads anteriorly, lying at first over and then mesial to the columella. It joins the r. jugularis facialis as this separates from the r. hyomandibularis facialis. Its relationship to the head vein can be seen from text-fig. 9. The arrangement is generally the same in other members of the urodeles.

(g) *The glossopharyngeal nerve IX.* The r. post-trematicus IX runs posteriorly and then vertically close to the lateral border of branchiale I. It lies behind gill slit I and runs forward ventral to branchiale I. The r. pharyngeus IX runs ventro-anteriorly from its origin, at first lateral and then gradually mesial to the lateral dorsal aorta, underneath the auditory capsule and over the pharynx. No pretrematicus is recognizable in this or any other stage examined. The r. post-trematicus innervates the M. levator arcus branchialis I, possibly also the M. ceratohyoideus externus, and terminates in the M. ceratohyoideus internus.

Fig. 20.



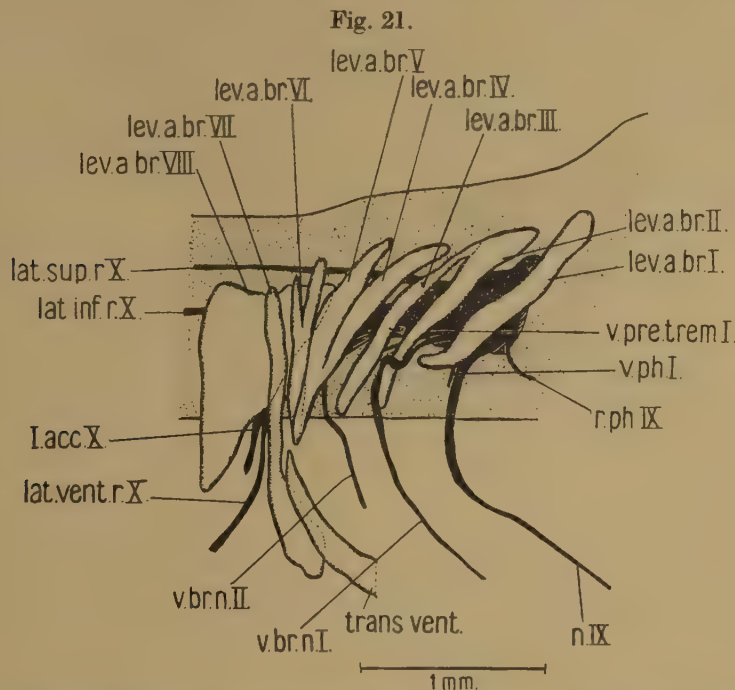
32 mm. stage. Lateral reconstruction of the vagus trunkus intestino-accessorius X, with the glossopharyngeal and seven vagus branchial nerves; the three lateralis nerves have been included. (Key to the references p. 296.)

(h) *The vagus nerve X.* A detailed consideration of the vagus branchial nerves and their musculature will be made in the account of the 32 mm. stage.

(i) *The vagus lateralis nerves X.* There is a r. lateralis superior arising from the dorso-mesial side of the vagus ganglion, a r. lateralis inferior arising from the mesial side, and a r. lateralis ventralis arising from the postero-lateral surface of the vagus. These nerves run posteriorly along the side of the body innervating the lateral line organs, and they are generally present in larvae and aquatic adults

among the urodeles. They are the same in the 26, 30 and 32 mm. stages of *Cryptobranchus japonicus* (Pl. 2, fig. 11 ; text-figs. 25, 26).

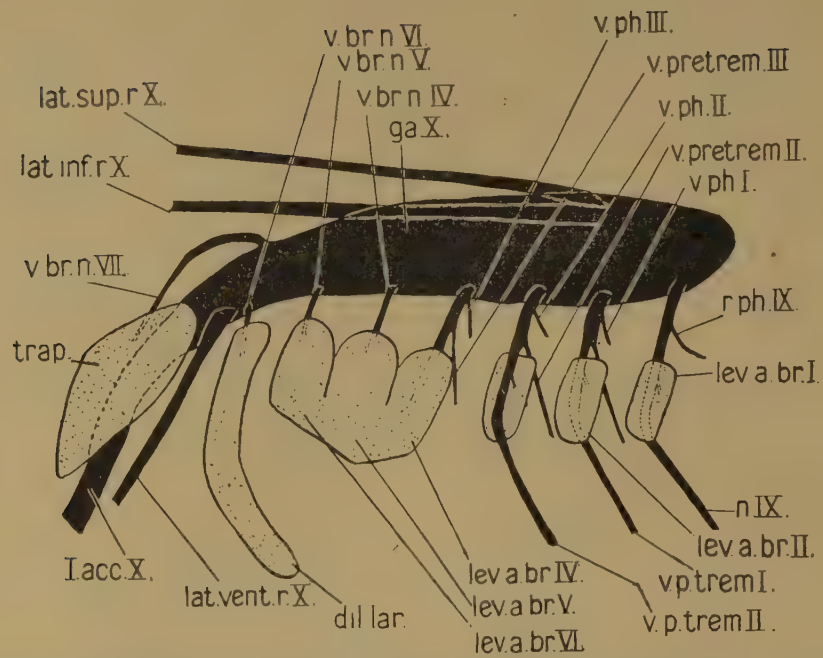
(j) *The hypoglossal nerve* runs ventro-laterally from its insertion on the ventro-lateral margin of the medulla, emerging via the foramen hypoglossus (Pl. 2, fig. 10). It divides into an upper ramus which runs mesial and close to the vagus ganglion to muscles above the latter, and a lower ramus which runs mesio-ventral to the vagus ganglion, to innervate the ventral region of the somite of the third metotic segment. It is well developed and distinct in the 17, 19, 26 and 32 mm. stages as well. The pre-occipital arch lies anterior to the foramen hypoglossus between the second and third metotic segments. These arches are serially homologous with the posterior neural arches (see text-fig. 27).



32 mm. stage. Lateral reconstruction of the musculature in the vago-pharyngeal region, with some of the branchial nerves exposed to view. (Key to the references p. 296.)

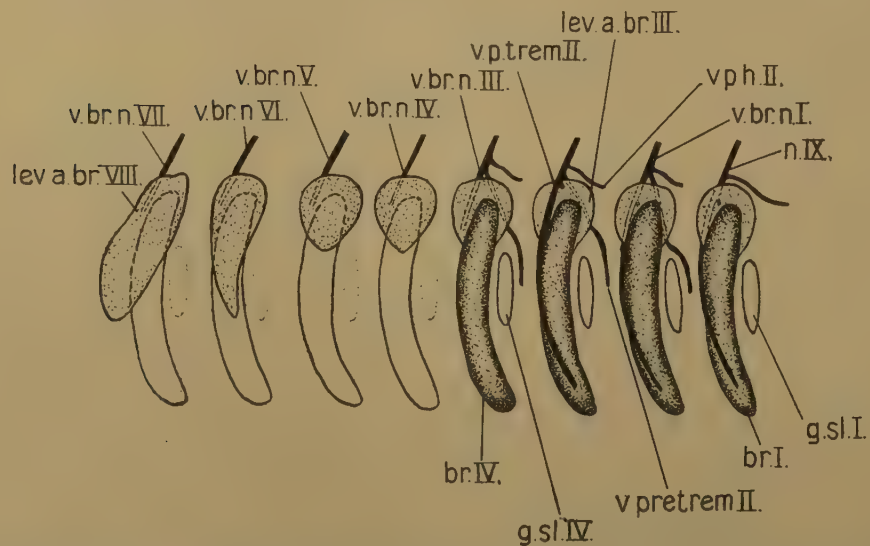
(k) *Spinal nerves I and II.* Spinal nerve I (30 mm. stage) emerges by two ventral roots from the ventro-lateral margin of the spinal cord, between the occipital and first neural arches. There is no dorsal root or ganglion. Spinal nerve I on the other side has a single broad insertion, which size being about the same as that of the other side. The vertebral artery runs through the insertion on the paired side. The ventral root of spinal nerve I divides into an upper and lower ramus which innervate the musculature of the fourth metotic segment. In the 15 mm. stage spinal nerve I has a dorsal root and ganglion. In the 19 mm. stage there is no dorsal root but a rudimentary ganglion is present ; spinal nerve I lies 320 microns behind the hypoglossal nerve and the only real difference between the two is one of size, the spinal nerve being a stouter structure. The condition in the 17 mm. stage is similar to that in the 19 mm. stage larva. The 26 mm.

Fig. 22.



Lateral diagrammatic representation of the branchial nerves and related Mm. levatores arcuum branchialum in the vago-pharyngeal region. (Key to the references p. 296.)

Fig. 23.



Theoretical representation of the glossopharyngeal-vagus pharyngeal region in some pre-amphibian types; the omission of the four posterior gill clefts and branchial arches demonstrates the condition in *Cryptobranchus japonicus* (32 mm. stage). (Key to the references p. 296.)

larva possesses a small concentration of nerve cells in the dorsal ganglion region (dorso-mesial to the upper ramus of the ventral root), and a vertebral artery runs through the insertion as in the 19 and 30 mm. stages.

Spinal nerve II is larger than spinal nerve I and possesses a ganglion and a dorsal root, the latter lying slightly caudal of the ventral root. The ventral root divides into an upper and a lower ramus which innervate the dorso and ventro-lateral musculature. It emerges between neural arches I and II when these are present in the 26 mm. and later stages.

A survey of the literature of the urodeles reveals the following information on the anterior spinal nerves; the r. hypoglossus is synonymous with the r. hypobranchialis.

In *Necturus* Fischer (1864) thought that the hypoglossal (hypobranchialis) nerve was formed from spinal nerves II and III, while spinal nerve I (ventral root only) had an independent course. Kingsbury (1895) disagreed with Fischer and considered that the first three nerves were spinal nerves I, II and III (the first spinal nerve was not a spinal accessory), and the area of the "hypoglossal" was supplied by some of their branches. Further, the first two nerves caudal of nerves IX and X have no dorsal roots and ganglia. Platt (1896 b) in a 12 mm. larva found that the two anterior spinal nerves have no dorsal roots but have small rudimentary ganglia at the base of the motor nerve. Norris (1911) and Norris & Buckley (1911) agree with Kingsbury except in finding that a branch only from spinal nerve III contributes to the "hypoglossal" nerve (spinal nerves I and II). In *Spelerpes* spinal nerve I arises from two ventral roots dividing into a dorsal ramus (innervating the M. longissimus dorsi) and a ventral ramus. The hypoglossus is formed chiefly though not entirely from spinal nerve I (Bowers 1900, Norris 1911).

In *Amblystoma* spinal nerve I arises from two ventral roots and a small ganglion is present. Spinal nerves I and II join together to innervate the M. sternohyoideus and M. geniohyoideus (Coghill 1902). Drüner (1904) found no ganglion or dorsal root to spinal nerve I. Kingsley (1902 a) seems to reconcile these results when he reports that in the larval *Amblystoma jeffersonianum* and *punctatum* spinal nerve I has a ganglion and dorsal and ventral roots, but in the 45 mm. specimen of the latter only the ventral roots can be found. However, Goodrich (1911) found spinal nerve I emerging from the skull between the latter and the first neural arch as a ventral root only. It joins the complete spinal nerve II and these together form the hypoglossal nerve which innervates the muscles derived from the ventral outgrowths of the second, third and fourth myotomes (third, fourth and fifth metotic segments).

In *Siren* spinal nerve I issues by two ventral roots and divides into a dorsal and ventral ramus (Norris 1913). The ventral ramus joins the ventral ramus of spinal nerve II and together these nerves form the hypobranchial nerve (Norris 1913, Drüner 1904).

In *Cryptobranchus japonicus* adult, spinal nerve I issues by a ventral root only and innervates the M. sternohyoideus and M. geniohyoideus (Osawa 1902, Drüner 1904). Drüner further describes the hypobranchial nerve as being formed from spinal nerves I, II and III. Spinal nerve I has no dorsal root or ganglion in the adult *Cryptobranchus alleghaniensis* (Drüner 1904). The absence of dorsal roots to spinal nerve I was reported by McGregor (1896). *Elipsoglossa* has no ganglion or dorsal root to spinal nerve I (Drüner 1904). In *Amphiuma* spinal nerve I arises from two dorsal and two ventral roots, and several small nerves arise from a ganglion and pass dorsally to the longissimus dorsi (Kingsley 1902 a). Drüner (1904) in older specimens found no ganglion to spinal nerve I. Norris (1908) has analysed the arrangement in detail. In the 120 mm. stage there are two dorsal and two ventral roots and a small ganglion present to spinal nerve I. In the 140 mm. stage there are no dorsal roots but a small ganglion is still present. In the 175 mm. stage there are neither dorsal roots nor ganglion. Furthermore spinal nerves I and II are completely separate, the hypoglossus nerve being spinal nerve I. The latter innervates the M. sternohyoideus, M. geniohyoideus and M. genioglossus. The gradual loss of the dorsal roots and ganglion to spinal nerve I during ontogeny in *Amphiuma* should be borne in mind when *Cryptobranchus japonicus* is considered.

In *Salamandra* Francis (1934) calls spinal nerve I the nervus suboccipitalis, stating that it is only a transient structure. The "hypoglossus" is formed from spinal nerves II and III.

In general in the urodeles spinal nerve II possesses a ganglion and dorsal and ventral roots. The exceptions to this rule appear to be *Necturus*, where spinal nerves I and II possess ventral roots only (Norris 1911, Norris & Buckley 1911), and *Salamandra*, where the true spinal nerve II arises by two ventral roots only in the adult, but the larva has a dorsal root and ganglion (Francis 1934).

(1) *The r. intestino-accessorius X*. A general account will be given of the results obtained in the 26 and 30 mm. stages of *Cryptobranchus japonicus*. In this account spinal nerve I is synonymous with the r. hypobranchialis.

The r. intestino-accessorius X divides into the following branches: (1) r. lateralis ventralis, (2) three rami intestinales, i.e. r. gastricus, and two gastrotracheal branches, (3) r. intestinalis recurrens, (4) r. laryngeus recurrens, (5) several fine cardiac branches (Pl. 2, fig. 11; figs. 25, 26).

(1) The r. lateralis ventralis runs posteriorly lateral to the r. hypobranchialis lying lateral and close to the auricle. Proceeding posteriorly it gradually inclines ventrally, passing the "anteriorly running" spinal nerve II. It comes into contact with the latter in both the 26 and 30 mm. stages, but a definite anastomosis is only seen in the 26 mm. stage. The r. lateralis ventralis proceeds posteriorly, lying on the surface of the lateral plate.

(2) The rami intestinales X include a large gastric branch leading posteriorly to the dorsal surface of the oesophagus, and two lateral rami (which may anastomose with each other). These lateral rami lie between the oesophagus and the origin of the paired bronchi. The position of these endings between the oesophagus and trachea suggests that it would be appropriate to call them gastrotracheal nerves. Posteriorly the oesophagus and bronchi lie in close apposition to one another and the nerves lie between them.

(3) The ramus intestinalis recurrens X runs antero-mesial to the r. hypobranchialis. It is separate from spinal nerve I in the adult *Cryptobranchus japonicus* (Osawa 1902), but anastomoses with it in *alleghaniensis* (McGregor 1896). In the 26 and 30 mm. stages the nerves are separate and distinct.

(4) The r. laryngeus recurrens X is a small branch running anteriorly to the tissue below the trachea just anterior to the heart. It arises posterior to the r. intestinalis recurrens X as an anterior branch of one of the r. intestinales.

(5) The cardiac nerves are not clear in this material. An anterior branch arises from the r. intestino-accessorius X mesial to the r. hypobranchialis, lying just posterior to the r. recurrens intestinalis X. Several extremely delicate branches appear to be given off from the two lateral rami intestinales nerves; these fibres seem to lead to the heart.

(m) *The relationship of spinal nerve I to the r. intestino-accessorius X*. Spinal nerve I is completely separate from spinal nerve II, as in *Amphiuma* (Norris 1908). Spinal nerve I proceeds posteriorly mesial to the r. intestino-accessorius X and then curves anteriorly lateral to the gastric branches. It receives a branch from the r. intestino-accessorius X in this 26 mm. stage; in *Amphiuma*, in contrast, Norris (1908) denies the occurrence of an anastomosis between hypobranchialis and vagus nerves. The spinal nerve I continues anteriorly mesial to the r. lateralis

ventralis X and lateral to the cardiac nerves. In the 32 mm. stage it lies above the lateral M. thoracohyoideus and mesial to the M. geniohyoideus and innervates them both (see text-figs. 24, 25, 26).

Blood vessels.

(a) *Veins antero-mesial to the processus ascendans.* A large dorsal vein originates mesial to the superior obliquus. It receives veins from the brain and the dorso-mesial surface of the eye. Posteriorly it lies mesio-ventral to the trochlear nerve, dorsal to the profundus and finally mesial to the latter and rectus muscles. It joins two other veins ventral to the r. ophthalmicus profundus V.

The middle vein originates ventro-mesial to the eye. Posteriorly it lies ventral to the rectus muscles, mesial to the truncus infraorbitalis, dorsal to the processus pterygoideus and ventro-lateral to the profundus. It then joins the upper and lower veins.

The lower vein originates as a sinus ventral to the solum nasi. Posteriorly it lies ventral to the prevomer and the trabecula, mesial to the processus pterygoideus and lateral and close to the palatine nerve. It turns upwards to join the other two veins.

The single resulting vein leads posteriorly mesial to the processus ascendens and ventral to the profundus. On one side only, a small hypophysial vein emerges through a small foramen to join the main vein. Between the palatine nerve and the processus pterygoideus a vessel leads posteriorly close to the wall of the tympanic pouch. The vena capitis medialis joins the vena capitis lateralis over the dorso-anterior surface of the processus oticus and lies dorso-lateral to the columella, mesial to the squamosal. It receives several vessels along its course. The head vein continues posteriorly mesial and then ventro-mesial to the connective of Willis on the ventro-lateral surface of the auditory capsule. On reaching the foramen metotica it receives two post-cerebral veins emerging from the skull. The larger vein emerges over ganglion IX, joining the head vein just posterior to nerve IX, the smaller vein emerges from below the brain ventral to ganglion IX (text-fig. 13).

(b) *Veins antero-lateral to the processus ascendens.* The vena capitis lateralis arises as a sinus ventral to the truncus infraorbitalis. It receives the optic vein emerging from the skull through the foramen optica and posteriorly it lies ventral to the truncus infraorbitalis, dorso-lateral to the processus pterygoideus and lateral to the temporalis muscle. It continues lateral to the r. mandibularis V and dorsal to the masseter muscle before joining the vena capitis medialis. Before joining the latter it receives a large dorsal vein from the dorso-lateral region of the orbit and brain (text-fig. 13).

(c) *The arteries.* Efferent epibranchial artery I (aortic arch II) joins the lateral dorsal aorta mesial to the pterygo-quadrate (text-fig. 15). Posteriorly it lies ventral to the head vein and lateral to the palatine nerve. It dips down ventrally mesial to the anterior region of the squamosal and the r. mentalis externus facialis, and lateral to the hyoid. The lateral dorsal aorta proceeds posteriorly ventro-lateral to the columella, ventro-mesial then lateral to the head vein. About 30 microns

posterior to the foramen hypoglossus the lateral dorsal aorta receives efferent epibranchial artery II (text-fig. 13).

Efferent epibranchial artery II runs postero-laterally for 220 microns and then dips down vertically behind gill slits I and II, mesial to branchiale I. Efferent epibranchial artery III joins the lateral dorsal aorta 300 microns posterior to the preceding artery. It runs postero-laterally for about 180 microns and then mesio-ventrally to the posterior edge of branchiale II, behind gill slits II and III.

Efferent epibranchial artery IV joins the mesial surface of epibranchial artery III. It runs postero-laterally between branchiale III and IV, behind gill slits II and III.

Efferent epibranchial artery V joins the mesial surface of epibranchial artery IV. It lies behind gill slit IV.

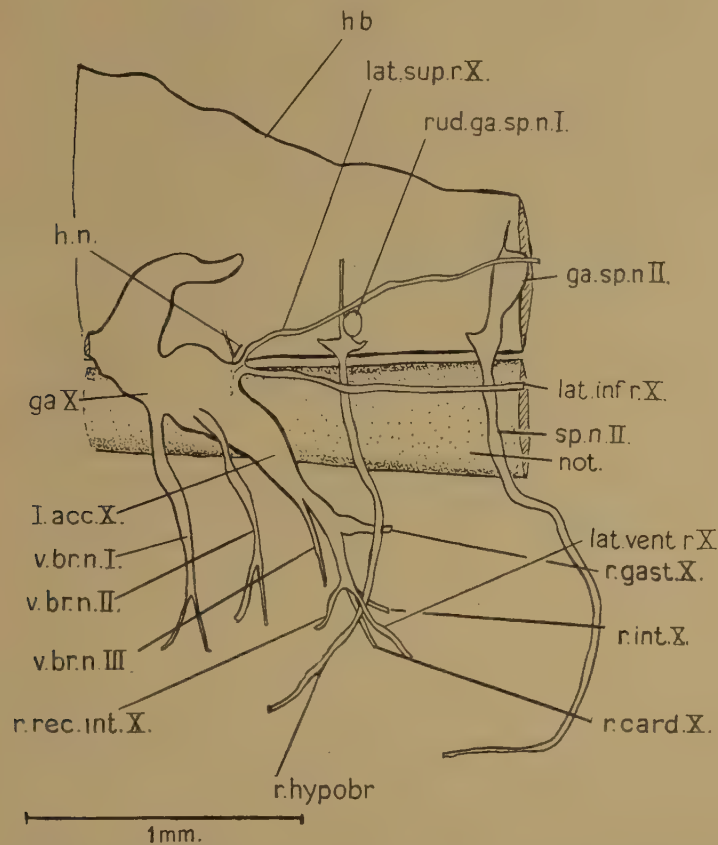
The lateral dorsal aortae meet behind the epibranchial arteries forming the median dorsal aorta.

The internal carotid artery turns upwards at the crista sellaris alongside the pituitary region (text-fig. 15). It runs antero-dorsally inside the chondrocranium. A supraorbital artery (homologue of the ophthalmica magna artery of *Ceratodus*, De Beer 1926) emerges via the foramen oculomotorius beneath nerve III. It crosses the orbit beneath the profundus nerve leading to the median surface of the eye. Anteriorly the internal carotid gives off a large cerebral branch dorsally, alongside the anterior mid-brain. From the plexus (formed from both sides) a pair of posterior carotid cerebrealis vessels arise which meet below the hind-brain as the artery basalis. The anterior paired carotid cerebrealis vessels lie alongside the fore-brain, the ventral artery leading to the ventral surface between the anterior ends of the trabeculae, while the upper artery leads between the olfactory lobe and the rest of the fore-brain. It meets its fellow from the other side, forming a plexus. Just anterior to the crista sellaris a palatine artery arises from the internal carotid. It lies below the parasphenoid above the roof of the mouth. It is absent in elasmobranchs, rarely present in teleostomes but present in the Dipnoi (Goodrich 1930).

The ciliary ganglion. Herrick found no ciliary ganglion in *Amblystoma punctatum* though in *A. tigrinum* it is a transient structure and probably never functional (Coghill 1902, Kunz 1914). It is absent in *Necturus* (McKibben 1913) and *Amphiuma* (Norris 1908), while Osawa (1902) in *Cryptobranchius japonicus* was not convinced of its presence. Bowers (1900) in *Spelerpes bilineatus* found a cluster of cells constantly enveloping that part of nerve III which lies directly underneath the optic nerve. In her 23 mm. stage these cells are in a compact mass, but in the 40 mm. stage they are scattered along the nerves. In *Salamandra*, where nerve III divides, a slight swelling represents the ciliary ganglion (Francis 1934). In *Triton taeniatus* ganglion cells are connected more or less distinctly with the rami of nerve III but their occurrence seems to have wide variation. These cells represent the ciliary ganglion belonging to the sympathetic, having some physiological significance (Coghill 1906). Kunz (1914) in *Amblystoma* larvae describes a slender nerve III arising ventrolaterally from the mesencephalon accompanied by a few large cells. In his 13 mm. stage the nerve is traced into the orbit where it ends among mesenchyme (early eye muscles). Near the tip of nerve III a few large nuclei are seen, these being almost identical with the nuclei of the cells surrounding the oculomotor nerve. The number of cells at the tip does not increase appreciably during development and no fibre connection can be seen with the gasserian ganglion.

The results in this paper seem to agree with those of Kunz. In the 26 mm. stage slender nerve III is ensheathed by several oval or elongated nuclei. There is a small collection of nuclei similar to the ensheathing nuclei at the origin of the superior and inferior rami. The 30 and 32 mm. stages are similar. In the 19 mm. stage nerve III may possibly be present on one side. It is extremely short, not reaching as far as the mesenchyme in the orbit, and it appears to end in a small cluster of cells (50 microns antero-posteriorly). Whether this is a ciliary ganglion in rudimentary form cannot be decided.

Fig. 24.



19 mm. stage. Lateral reconstruction of the vagus ganglion, vagal and spinal nerves I and II. The hypoglossal nerve is included. (Key to the references p. 296.)

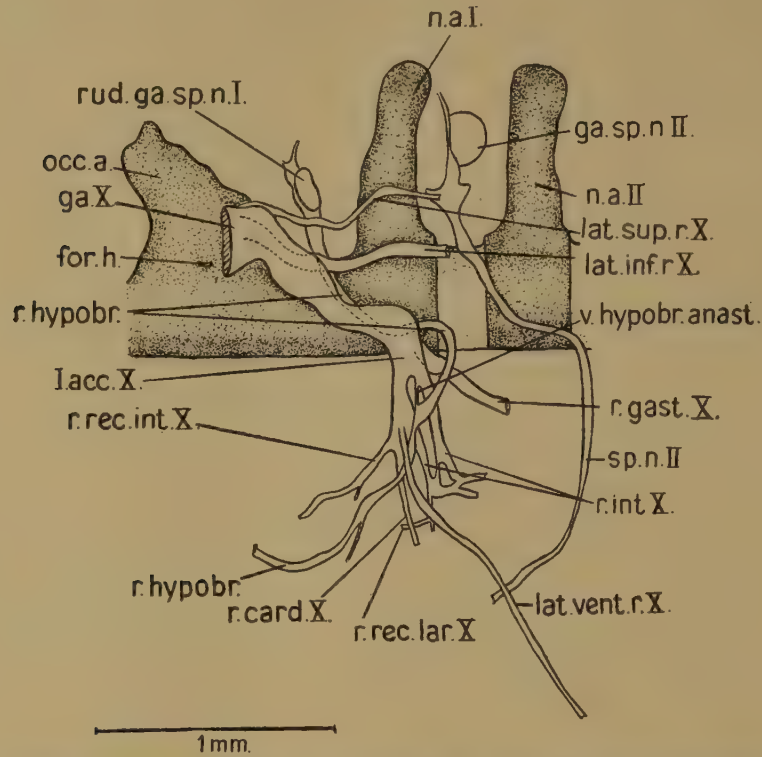
(f) The vagus branchial nerves and musculature in the 32 mm. stage larva.

In *Siren*, Norris (1913) reported four vagus branchial nerves. Three vagus nerves were described in *Necturus* (but the third is reduced) (Norris & Buckley 1911), *Plethodon* (Dodds 1906), and *Amphiuma* (Kingsley 1902 a), though Norris (1908) reported only two in the latter. There are two vagus nerves in *Amblystoma* (Coghill 1902), *Triton* (Coghill 1906), *Salamandra* (Francis 1934) and *Cryptobranchus japonicus* adult (Osawa 1902), though Drüner (1904) reported four "Kiemenbogen Nerven" (nerves IX and three vagus), with the last vagus nerve merely a rudiment. *Spelerpes* has only one vagus nerve, the second being reduced (Norris 1911).

The vagus branchial nerves and musculature (text-figs. 20, 21, 22, 23).

Nerves. The vagus branchial nerve I includes a ramus pretrematicus, pharyngeus and post-trematicus; the pretrematicus lying mesial to the post-trematicus. The latter lies ventral to the M. levator arcus branchialis II which it innervates. It then curves over the dorsal end of branchiale II and runs anteriorly, lateral and ventral to the latter (Pl. 3, fig. 2).

Fig. 25.



26 mm. stage. Lateral reconstruction of the vagus ganglion, truncus intestino-accessorius X and spinal nerves I and II. The three lateralis vagus nerves are included and the whole is considered in relation to the occipital arch and the two anterior neural arches. (Key to the references p. 296.)

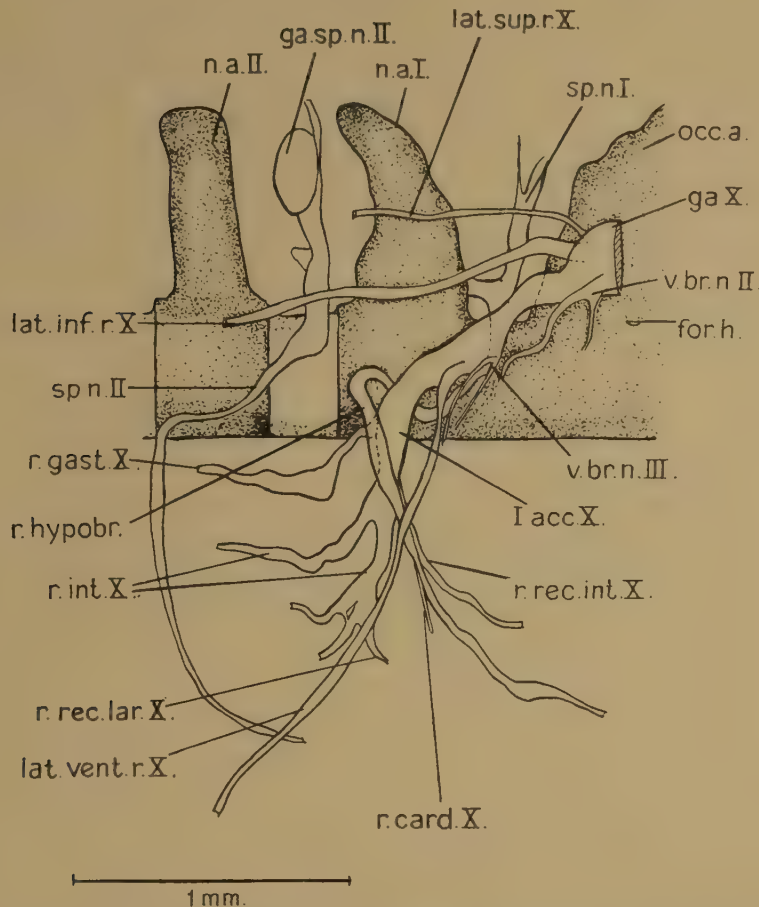
The vagus branchial nerve II includes a ramus pretrematicus, post-trematicus and pharyngeus, present on one side, while the r. pretrematicus is missing on the other side. However, the typical condition of vagus branchial II is one in which the three rami are present. The r. post-trematicus on one side runs postero-laterally over the M. levator arcus branchialis III, while on the other side it lies ventral to this muscle. This difference is probably without phylogenetic significance. The r. post-trematicus leads over the dorsal surface of branchiale III lying behind gill slit III, and then runs antero-ventrally, lateral and ventral to branchiale III. It innervates the M. levator arcus branchialis III (Pl. 3, fig. 3).

The vagus branchial nerve III includes a ramus pretrematicus, post-trematicus and pharyngeus on one side only, while on the other side there is only a r. post-trematicus. This difference will be considered again later. The r. post-trematicus

does not curve round anteriorly as do the preceding vagus nerves, but ends in and innervates the *M. levator arcus branchialis IV*, ending in the ventro-mesial surface (Pl. 3, figs. 4, 5).

The vagus branchial nerve IV lies 120 microns posterior to the vagus branchial nerve III on one side, and 100 microns posterior to the latter on the other side.

Fig. 26.



30 mm. stage. Lateral reconstruction of the vagus ganglion, some of the vagus nerves, the truncus intestino-accessorius X and the spinal nerves I and II. The three lateralis vagus nerves are included and the whole is considered in relation to the occipital arch and the two anterior neural arches. (Key to the references p. 296.)

It is 220 microns long on one side and 130 microns long on the other, being merely a single post-trematic strand on both sides. The slender nerve leads to and innervates the *M. levator arcus branchialis V* (Pl. 3, fig. 5).

The vagus branchial nerve V is a single strand emerging from the lateral surface of the vagus ganglion. It is an extremely delicate nerve and innervates the *M. levator arcus branchialis VI* (Pl. 3, fig. 6).

The vagus branchial nerve VI is seen distinctly on one side only and it innervates that *M. dorso-laryngeus* on its mesial surface. The vagus branchial nerve VI lies just anterior to the origin of the *r. lateralis ventralis X* (Pl. 3, fig. 7).

The vagus branchial nerve VII arises from the dorsal surface of the vagus ganglion anterior to the region where spinal nerve I crosses over the r. intestino-accessorius X; at approximately the level of the vagus branchial nerve V. It lies mesial to the muscle it innervates, lateral to the head vein, and running posteriorly over the vagus ganglion it innervates the tapezius. The nerve is plainly visible on the two sides of the head, being approximately 150 microns long (Pl. 3, fig. 8).

Muscles (see Pl. 3, figs. 1-8; text-fig. 21). The M. levator arcus branchialis I originates anteriorly, dorso-lateral to the auditory capsule. It leads postero-ventrally lying over nerve IX (r. post-trematicus IX), and the M. ceratohyoideus externus. It ends with the latter at the dorsal posterolateral surface of branchiale I and is innervated by nerve IX.

The M. levator arcus branchialis II is similar to the preceding muscle. It inclines postero-ventrally over the vagus branchial nerve I (post-trematicus), and just after the latter has curved underneath the muscle to lead to the lateral surface of branchiale II, the M. levator II is inserted on the dorso-mesial surface of this arch. It is innervated by vagus branchial I.

The M. levator arcus branchialis III originates anteriorly with the preceding muscle. It separates from the latter dorsally and then runs postero-ventrally, lying underneath the vagus branchial nerve II on one side and over the latter nerve on the other side. It is inserted on the mesio-dorsal surface of branchiale III and is innervated by the vagus branchial nerve II.

The M. levator arcus branchialis IV runs postero-ventrally lying over the vagus branchial nerve II and the preceding M. levator III, and ends on the mesio-posterior surface of branchiale IV. It is innervated by the vagus branchial nerve III whose r. post-trematicus III ends in the muscle.

The M. levator arcus branchialis V originates separately from the M. levator IV. It leads postero-ventrally and is inserted mesial to the posterior surface of the preceding muscle. It is innervated by the vagus branchial nerve IV.

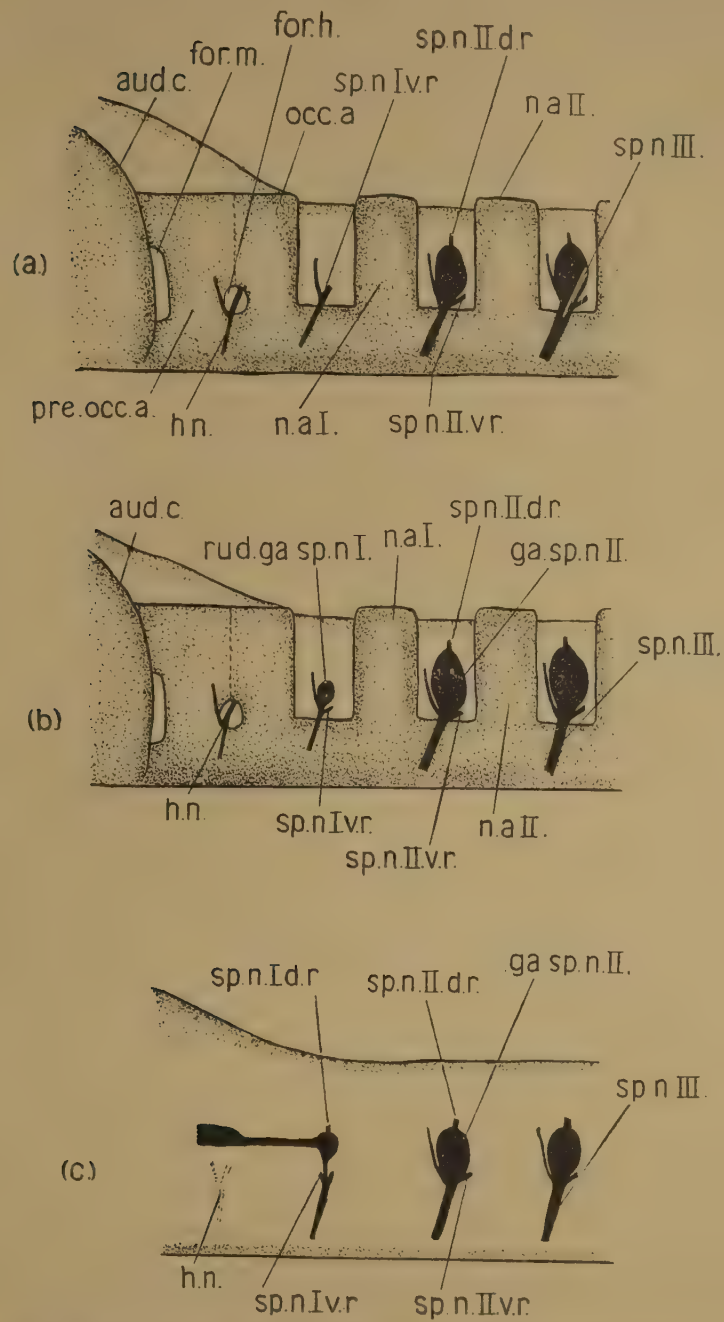
The M. levator arcus branchialis VI originates independently at its anterior end, and lies almost dorso-ventrally behind the M. levator V. It is intimately associated with the latter muscle, lying against its mesio-posterior surface. It is innervated by the vagus branchial nerve V. The ventral border of the M. levator VI lies close to a large ventral muscle; probably the latter is the posterior edge of the M. transversus ventralis.

The M. dilator-laryngeus (dorso-laryngeus) is a large muscle extending dorso-ventrally alongside the posterior region of the pharynx, lying posterior to the preceding muscles. It is inserted on the ventro-lateral surface of the larynx, and is innervated by the vagus branchial nerve VI.

The trapezius is the most posterior pharyngeal muscle (i.e. the eighth counting the glossopharyngeal segment as the first). It arises mesially to the two preceding muscles and extends posteriorly as a sheet-like tissue. It is the largest muscle of the series and it is innervated by the vagus branchial nerve VII.

All the muscles of this series are flattened and sheet-like, lying lateral to the vago-pharyngeal region.

Fig. 27.



Diagrammatic representation of the occipital and anterior neural arches, together with the hypoglossal (spino-occipital) and anterior spinal nerves in :

(a) 30 mm. stage.

(b) 26 mm. stage (19 mm. stage is the same without the cartilage).

(c) 15 mm. stage (the hypoglossal nerve is present by the 17 mm. stage).

(Key to the references p. 296.)

<i>Muscle</i>		<i>Nerve</i>		<i>Cartilage Bar</i>	<i>Gill Slit</i>
levator arcus branchialis	I	IX		branchiale I	I
levator arcus branchialis	II	vagus branchial nerve	I	branchiale II	II
levator arcus branchialis	III	vagus branchial nerve	II	branchiale III	III
levator arcus branchialis	IV	vagus branchial nerve	III	branchiale IV	IV
levator arcus branchialis	V	vagus branchial nerve	IV	—	—
levator arcus branchialis	VI	vagus branchial nerve	V	—	—
dilator-laryngeus muscle		vagus branchial nerve	VI	—	—
trapezius muscle		vagus branchial nerve	VII	—	—

DISCUSSION.

The phylogenetic significance of the branchial nerves and musculature.

From the examination of the 32 mm. stage in *Cryptobranchus japonicus* we know that during ontogeny there is a glossopharyngeal nerve IX, and behind in sequence emerging from the vagus ganglion are seven vagus branchial nerves. The arrangement is almost identical on both sides of the head. We know further that nerve IX is associated with the branchiale I segment, while the following three vagus nerves are related to the next three posterior branchial arches. The glossopharyngeal and the three vagus branchial segments have gill clefts (open to the exterior), branchial cartilage bars, and branchial musculature (levator arcus branchialis muscle, together with the M. ceratohyoideus externus in the glossopharyngeal segment). The corresponding nerves have a ramus pretrematicus, post-trematicus, and pharyngeus, except nerve IX which has no r. pretrematicus.

Vagus branchial nerves IV, V, VI and VII are single strands only, each innervating their respective muscles. The question is, are these posterior nerves serially homologous with the anterior branchial nerves? It seems indisputable that this is the case. A study of their arrangement and distribution shows that they are branchial nerves which have lost their pretrematic and pharyngeus rami, while the ramus post-trematicus ends in the muscle associated with it and does not curve forwards anteriorly. We find that the vagus branchial nerve III resembles these more posterior branches in that it does not curve forwards anteriorly but ends in the M. levator arcus branchialis IV. Further we may note that in this 32 mm. specimen the vagus nerve III on one side has the three typical rami, while on the other side there is only a ramus post-trematicus III ending in the muscle.

On considering the series of muscles lying lateral to the primary somites of the pharyngeal region we may note that each one is innervated by a branchial nerve. Reference to the reconstructions suggests serial homology. According to Goppert and to Goodrich, a muscle never changes its innervation during the course of phylogenetic history. If they are correct their view helps to support the suggestion of the serial homology of these levator muscles. Certainly, the remarkably uniform serial arrangement of eight separate muscles innervated by eight separate serially homologous branchial nerves is too clear-cut to be mere coincidence. If the Mm. levatores arcuum branchialum I, II, III and IV are serially homologous, then Mm. levatores arcuum branchialum V, VI, VII and VIII are serially homologous also. If this is true, then the M. dilator-laryngeus and the M. trapezius although

having different functions in the higher vertebrates are the homologues of two branchial muscles from a fish-like ancestor. Goppert (1894) thought that the *M. dilator-laryngeus* in urodeles was a *M. levator arcus branchialis V* homologous with the levatores of the other branchial arches, but Drüner (1901) regarded the *M. dilator-laryngeus* as serially homologous with the *Mm. levatores arcuum branchialum*, though of a segment posterior to the fifth branchial segment. Edgeworth (1923 b, p. 104), in *Cryptobranchus* finds only four *Mm. levatores arcuum branchialum*, the *M. levator arcus branchialis IV* being followed by the *M. dorso-laryngeus* (dilator-laryngeus) and the *M. trapezius*. From these results in this paper it would seem that Edgeworth's *M. levator arcus branchialis IV* is in reality the *Mm. levatores arcuum branchialum IV, V, VI* fused together, there being two complete segments between the *M. levator IV* and the *M. dorso-laryngeus* (text-fig. 22).

To return to the posterior pharyngeal region, we may note that in the larval *Cryptobranchus japonicus* the *Mm. levatores arcuum branchialum IV, V* and *VI* show intimate association in their ventral region, suggesting that the posterior muscles have moved forwards somewhat, so making it possible for them to have an insertion on the branchiale IV.

Segment	Nerve	Branchial skeleton	Gill cleft	Muscle
Nerve IX	r. pharyngeus r. post-trematicus	branchiale I	open	ceratohy. externus levator a. br. I
X. branchial I	r. pharyngeus r. pretrematicus r. post-trematicus	branchiale II	open	levator a. br. II
X. branchial II	r. pharyngeus r. pretrematicus r. post-trematicus	branchiale III	open	levator a. br. III
X. branchial III	r. pharyngeus r. pretrematicus r. post-trematicus	branchiale IV	open	levator a. br. IV
X. branchial IV	r. post-trematicus (to muscle only)	absent	small vestige Menopoma, small vestige Cryptobranchus	levator a. br. V
X. branchial V	r. post-trematicus (to muscle only)	absent	small vestige Menopoma	levator a. br. VI
X. branchial VI	r. post-trematicus (to muscle only)	absent	—	levator a. br. VII (dilator-laryngeus)
X. branchial VII	r. post-trematicus (to muscle only)	absent	—	levator a. br. VIII (trapezius)

Now if we assume that a complete branchial segment contains a nerve, a muscle, a branchial arch and a gill slit, let us consider the posterior half of the branchial region. There are four vagus branchial nerves, IV, V, VI and VII, which innervate four separate muscles, apparently segmentally arranged behind the more

anterior muscles. We can thus assume that if the nerves are branchial nerves serially homologous with the more anterior vagus nerves, and if the muscles are branchial muscles segmentally arranged and serially homologous with the more anterior Mm. levatores arcuum branchialium, then it is fair to assume that these are parts of incomplete branchial segments which at some age in the past were complete branchial segments in a fish-like aquatic ancestor (text-fig. 23).

The possibility that posterior gill pouches which were present in some urodele ancestor have been lost during the course of phylogeny and do not appear during ontogeny, is not surprising. Gill clefts which are functional in the larva close up and are absent in the adult. In *Menopoma alleghaniensis* one small slit remains open, while even this is closed in the Japanese species. In the terrestrial salamanders and tritons there are no open gill clefts in the adult, though clefts are present in the larva. In the permanently aquatic neotenous *Proteus*, *Necturus*, and *Siren*, functional gill slits are retained.

The branchial arches are reduced in number during ontogeny. The adult *Cryptobranchus japonicus* has two branchial arches only (excluding the hyoid) (Osawa 1902, Hyrtl 1865, Drüner 1904). The larval form has four pairs of branchial arches (Edgeworth 1923 b, Fukuda 1928, Aoyama 1930), which agrees with our results. Two posterior arches are thus lost during ontogeny. In the larva of *Typhlotriton* there are only three branchial arches instead of four found in other members of the Desmognathidae (Hilton 1909), while the larval *Spelerpes bilineatus* has only three branchial arches (Smith 1920). Thus even among the larvae in urodeles some have three arches while others have four arches, suggesting that branchial arches are lost from ontogeny. There cannot then be any objection to postulating the loss of posterior branchial arches during the course of phylogeny.

In the same manner we may note that branchial nerves are reduced or lost during ontogeny. The aquatic urodeles (Perennibranchiata and early larval forms of Caducibranchiata) have more branchial nerves than the terrestrial adult forms. This is understandable, for they have a functionally developed gill slit region. In the metamorphosed adults there is reduction in this region (Norris 1913). Norris showed that in the adult *Siren* the fourth and fifth branchial nerves are reduced, and to some extent the third also. They are replaced functionally by the r. intestinalis recurrens X. Osawa (1902) showed only two pairs of vagus branchial nerves in the adult *Cryptobranchus*, but the 32 mm. stage of my series possesses seven pairs of vagus nerves. The more posterior nerves must be either extremely small or missing completely in the adult, otherwise Osawa would certainly have reported them. Thus if branchial nerves are reduced or lost during ontogeny in the urodeles, then one can accept a postulate that during phylogeny posterior vagus branchial nerves have become reduced, losing their ramus pharyngeus and pre-trematicus.

The musculature and gill clefts (or pouches) remain to be considered. We have postulated that the muscles are serially homologous and in fact they retain in the 32 mm. stage a somewhat primitive segmental pattern, which to some extent is undisturbed as yet by the radical rearrangement and fusion which takes place as development proceeds (text-fig. 21).

In the case of the gill clefts we must look for evidence which supports the view that posterior gill clefts (or pouches) existed in some ancestral form and have been lost during phylogenetic history. Edgeworth (1920) showed that in *Menopoma* during ontogeny there are five branchial segments (hyoid and four other branchial segments), plus two rudimentary segments VI and VII on one side only. Segments VI and VII are represented by rudimentary gill clefts which are soon lost and never become functional. In this present work the 17 mm. stage larva has five pairs of gill plugs, the fifth well developed on one side and only faintly developed on the other. In the 19 mm. stage there are five gill plugs on one side only and four on the other, and in the 26 and 32 mm. stages there are four pairs of functional gill clefts (open to the exterior), and on one side only, a small down-growth behind branchiale IV which is certainly a vestigial gill pouch. A similar trace of a gill slit lying between levatores arcuum branchialum IV and V was found by Drüner (1901) in *Triton* larvae. This evidence suggests that there were posterior gill pouches behind the fourth functional gill slit of the larva of *Cryptobranchus*, in some ancestral form.

A study of the formation of the lung does not concern us in this paper but it may be mentioned that in the 15 mm. stage there is a well-formed laryngeal groove, developed as a ventral diverticulum from the floor of the posterior region of the pharynx. In this stage there is a faint suggestion of a paired origin of this outgrowth. In the 17 mm. stage the ventral diverticulum is still not separated from the floor of the pharynx, but in the 19 mm. stage complete separation has occurred, and the larynx appears as a mesenchymatous mass of cells, which contain many large yolk globules. In the 26 mm. stage the larynx (and trachea) is well-developed, lying below the pharynx. If Edgeworth is correct, in *Menopoma* there are rudimentary gill clefts V and VI (excluding the hyoid segment), co-existing with the larynx. Thus the lung segment developed from the laryngeal groove is posterior to branchial segments V and VI. It is in fact in the seventh segment. We reach the same conclusion by a study of the 32 mm. stage *Cryptobranchus japonicus*. Here the M. dilator-laryngeus is innervated by the vagus branchial nerve VI, the latter muscle being inserted against and below the arytenoid cartilage of the larynx. This suggests that in urodeles the lungs were developed from branchial segment VII gill pouches, and there is the possibility that the arytenoid cartilages are modified branchiale VII.

The origin and development of the lungs in the early ancestors of the tetrapods can be suggested. A posterior pair of pouches (probably the seventh pair in the urodele phylogeny) arising from the ventro-lateral margin of the pharynx gradually meet near the mid-line during the course of phylogeny. No doubt these failed to break through to the surface of the body much earlier in phylogenetic history, and this would be possibly true for the eighth pair of pouches also. The eighth pair of pouches were probably lost very early in the phylogenetic history of the vertebrates, but they may have been squeezed out of existence by the developing lungs. In the course of phylogenetic history the seventh pair of gill pouches meet one another and proceed to form a laryngeal groove, this groove being the first stage in the formation of the lung; though no doubt the paired pouches

throughout the posterior region had a respiratory surface. Further development produced a respiratory air sac which was present as far back as the Devonian among the placoderms. It was no doubt a comparatively easy process for the animal to modify the fish-like respiratory buccal force pump mechanism to force air into the lungs. Later phylogenetic development merely increased the size and complexity of the air sac, the blood supply improved and the result was the tetrapod lung.

One point must be considered regarding the claim that in the urodeles the lungs are developed from branchial pouches VII (with or without VIII). This need not necessarily apply to other vertebrate orders. It is assumed that in some ancestral form there were four pairs of posterior gill pouches behind the last functional gill slit, and the lung pouches in other vertebrates may have developed from any pair or even more than one pair. The lung may thus have a polyphyletic evolution in the vertebrates. Nevertheless, it is homologous throughout the phylum; homologous organs may arise from different segments in different animals (Goodrich 1911).

One might expect to see traces of more posterior slits among the large number of Stegocephalia known. The explanation is no doubt that in these fossil forms, gill clefts would not be found if they were not open to the exterior. If one assumes that these posterior gill pouches were never functional as such in the Amphibia, then this would account for the absence of traces of posterior branchial segments in the fossil Amphibia. Goodrich (1930, p. 489), says that the original number of slits in the ancestral gnathostome was not large, possibly only seven or eight including the spiracular. The evidence from this investigation suggests that urodeles evolved from ancestral types that had a spiracular gill cleft and eight branchial segments.

If one considers the ostracoderms of the Silurian and Devonian we find the following facts. *Cephalaspis hoeli* and *Kiaeraspis* have ten branchial fossae. *Boreaspis rostrata* also has ten, but there may be one or two more behind the tenth. The majority of cephalaspids have ten and in no cephalaspid are there more than eleven or twelve (Stensiö 1927, p. 150). *Kiaeraspis* appears to have eight further branchial sacs behind nerve VII (third of series) (Stensiö 1927, p. 161), but he described the latter as having a pre-spiracular, spiracular, hyoid, glossopharyngeal and six vagus gill sacs, ten fossae in all. Each fossa has a corresponding nerve and there are no pretrematic rami.

The Tremataspidae have ten branchial openings like the Cephalaspidae (Patten 1903). The number of branchial openings is variable in the Anaspida; eight in *Birkenia* and *Rhyncholepis*, ten in *Pterolepis*, and twelve to fifteen in *Pharyngolepis* (Kiaer 1924, p. 89).

The Pteraspidae are like the Osteostrachi, certainly greater than seven, the anterior and posterior fossae probably not making any recognizable impressions (Stensiö 1927, p. 325).

In the living agnatha, *Petromyzon* has seven gill slits (Kiaer 1924, Johnston 1905), nerve IX lying behind gill slit I, *Myxine* has six, and *Bdellostoma* varies between six and fourteen (Kiaer 1924). Kiaer further states that a large number

of branchial openings is primitive and the number has by degrees been reduced in the real fishes. He assumes the same may be true for cyclostomes and Anaspida. It is suggested that the numerical pattern of the head of the urodeles may have been laid down in some members of the Cephalaspidomorpha. The number of segments described in the *Cryptobranchus* larva seems to correspond to the number in some species of *Boreaspis rostrata*, although in most of the known Osteostraci, in the eleventh head segment, the branchial sac may be reduced or lost.

It must be remembered, however, that a type like *Kiaeraspis*, though a pregna-thostome, was nevertheless highly specialized and certainly could not have been the ancestor of the gnathostomes. The latter possibly evolved from osteostracan stock early in the history of the ostracoderms. Correlated with the loss of functional gill clefts in the urodele ancestors (pre-amphibian types) was the loss of the skeletogenous bar supporting the pharyngeal wall behind the gill cleft. All that the urodeles and the other Amphibia inherited was the musculature, concomitant nerves, and to some extent vestigial structures like rudimentary gill clefts seen during the ontogeny of *Cryptobranchus japonicus* and *Menopoma alleghaniensis* (Edgeworth 1920). By the time the Stegocephalia had evolved from their osteolepid ancestors many changes had taken place. Probably the last gill pouch had disappeared (branchial segment VIII), while the hyoid gill cleft had closed and the ear developed from this segment. The seventh pair of pouches probably developed into the lungs. Of the condition of pouches V and VI one can only assume that they were present in the early Amphibia at some stage during their ontogeny, but very likely in a rudimentary form. We can see traces of these gill pouches approximately 280,000,000 years later, when two rudimentary gill clefts are seen for a transitory period during the ontogeny of *Menopoma alleghaniensis*.

SUMMARY AND CONCLUSIONS.

1. The foregoing account presents observations on the development of the blood system, chondrocranium and hyobranchial skeleton, ossifications and neuromuscular system in six larval stages of *Cryptobranchus japonicus* (*Megalobatrachus maximus*), viz. :—15, 17, 19, 26, 30 and 32 mm. stage larvae.

2. The arrangement of the vascular system in general is similar to the basic pattern in the urodeles, as described by Goodrich (1930), though five "complete" pairs of lateral aortic arches are seen joining the paired ventral aortae to the paired dorso-lateral aortae. Aortic arches III, IV and V, however, form a plexus of vessels in the three pairs of external gill filaments.

3. The chondrocranium and hyobranchial skeleton in my larval stages have been compared with the descriptions of Aoyama (1930), Edgeworth (1923 a, b) and Fukuda (1928). In general the results agree with these descriptions, especially with that by Aoyama, but even at the 32 mm. stage no antorbital process was seen; the processus pterygoideus meets the trabecula cranii only. The condition is a primitive one (Edgeworth 1925), and the condition in *Amblystoma*, *Desmognathus*, *Spelerpes*, *Salamandrella* and *Ranodon*, where the anterior portion of the process does not develop beyond that of a cellular strand, can be derived from it.

The formation of the processus pterygoideus in the 26 mm. stage suggests that part at least is formed as an independent chondrification *in situ*.

In the series studied there is little development of the nasal capsule and no comparisons could be made.

4. The posterior region of the skull, which includes the occipital region and the anterior neural arches, has been analysed and the results related to the earlier views on the segmental arrangement of the metotic segments (Goodrich 1911, Platt 1896 a, b). The presence of a well-formed hypoglossal (spino-occipital) foramen and nerve in *Cryptobranchus japonicus* confirms the descriptions by Fürbringer (1897), Osawa (1902), and Aoyama (1930). The general similarity of the hypoglossal (spino-occipital) nerve with the anterior spinal nerves lends support to the view that the occipital arch consists of anterior neural arches incorporated into the back of the skull. The border between the preoccipital and occipital arches is defined by the hypoglossal foramen and its corresponding nerve.

5. Spinal nerves I and II and their relation to the truncus intestino-accessorius X have been investigated. The spinal nerves and their related metotic somites and neural arches are compared with the descriptions by Platt of *Necturus* (1896 a, b), and by Goodrich of *Amblystoma* (1911). Except for the presence of a dorsal root to spinal nerve I in the 15 mm. stage larva of *Cryptobranchus japonicus*, the results agree with those of Goodrich.

6. The cranial nerves have been investigated in some detail; their arrangement in the 30 mm. stage has been compared with that of various urodeles. In general, the pattern of the cranial nerves conforms to the basic plan described in the urodeles which are known.

7. The glossopharyngeal and vagus branchial region in the 32 mm. stage appear to show a segmental pattern of serially homologous elements, viz.:—branchial nerves and muscles. The evidence suggests the presence of vestigial branchial segments posterior to the fourth functional gill cleft. It is argued that these may have been present and perhaps complete in some pre-amphibian ancestor. A glossopharyngeal and seven vagus branchial nerves, their related levatores arcuum branchialum, gill clefts and skeletal elements have been analysed. It is suggested that the Mm. dilator-laryngeus and trapezius are homologous with the Mm. levatores arcuum branchialum VII and VIII.

It is tentatively suggested that the lungs are formed from the seventh branchial segment.

8. This work supports modern ideas on the segmental pattern of the head in urodeles.

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KEY TO THE REFERENCE LETTERING TO PLATES AND TEXT-FIGURES.

- a.c.c.a.*, anterior carotis cerebialis artery.
a.c.d., artery carotis dorsalis.
a.c.v., artery carotis ventralis.
ang., angular.
ant.cop., anterior copula.
aud.c., auditory capsule.
aud.ves., auditory vesicle.
a.vert., vertebral artery.

b.art., basilar artery.
b.p., basal plate.
br. I, II, III, IV, branchiae I, II, III, IV.
brs.r.o.p.V, branches of ramus ophthalmicus profundus V.
br.r.mand.V, branch from r. mandibularis V.

c.c.a., carotis cerebialis artery.
cerbr. I, II, III, IV, ceratobranchiale I, II, III, IV.
cerhy.int., ceratohyoideus internus muscle.
cerhy.ext., ceratohyoideus externus muscle.
col., columella auris.
cor., coronoid.
cr.sell., crista sellaris.
c.t., crista trabecula.
c.Will., connective of Willis (VII-IX connection).

d.a., dorsal aorta.
dent., dentary.
digast., digastric muscle.
dil.lar., dilator-laryngeus muscle.
d.p.V., deep profundus V.
d.ram.sp.n.II, dorsal ramus spinal nerve II.

e.e.a.I, efferent epibranchial artery I.
e.e.a.ass.h.a., efferent epibranchial artery associated with hyoid.
e.e.a. II, III, IV, V, efferent artery II, III, IV, V.
eth.col., ethmoidal column.
ext.na., external naris.

f.b., fore-brain.
fen.ac., fenestra acoustica.
fen.end., fenestra endolymphatica.
fen.ov., fenestra ovalis.
fen.per., fenestra perilymphatica.
fiss.met., fissura metotica.
for.h., foramen hypoglossus.
for.m., foramen metotica.
for.oc., foramen oculomotorius.
for.op., foramen opticus.

ga. V, VII, VIII, IX, X, ganglia trigeminus facialis, acousticus, glossopharyngeus, and vagus.
ga.sp.n. I, II, ganglion spinal nerve I and II.
gass.ga., gasserian ganglion.
geniohy., geniohyoid muscle.
g.sl. I, II, III, IV, gill slit I, II, III, IV.

h.a., hyoid arch.
h.b., hind brain.
h.n., hypoglossal nerve.
ht., heart.
h.v., head vein.
hyobr. I, II, hypobranchiale I, II.

I.acc.X, intestino-accessorius X.
i.c.a., internal carotid artery.
inc.p., incisura prootica.
infund., infundibulum.
intermand.post., intermandibularis posterius.
intermand.ant., intermandibularis anterior.
i.o.v., infraorbital vein.

lat.X, future lateralis nerves.
lat.ga. IX, X, lateralis ganglion IX, X.
lat.VII ga., lateralis VII ganglion.
lat.inf.r.X, lateralis ramus inferior X.
lat.sup.r.X, lateralis ramus superior X.
lat.vent.r.X, lateralis ramus ventralis X.
le., lens.
lev.a.br. I, II, III, IV, V, VI, VII, levator arcus branchialis I, II, III, IV, V, VI, VII.
l.d.a., lateral dorsal aorta.
long.dors., longissimus dorsi muscle.

mass., masseter muscle.
m.b., mid-brain.
Meck.c., Meckel's cartilage.

n.a.I, II, neural arches I, II.
n. III, VI, IX, nerves oculomotor, abducens, glossopharyngeus.
nas., nasal.
nas.s., nasal sac.
n.oc., oculomotor nerve.
n.op., optic nerve.
not., notochord.
n.v., nasal vein.

o.a., supraorbital artery.
occ.a., occipital arch.
oesoph., oesophagus.
o.l., olfactory lobe.

- ol.n.*, olfactory nerve.
o.p.ga., ophthalmicus profundus ganglion.
op.v., optic vein.
orb.c., orbital cartilage.
orb.v., orbital vein.

pal.a., palatine artery.
pal.br.r.o.p.V, palatine branch, ramus ophthalmicus profundus V.
pariet., parietal.
passp., parasphenoid.
p.c.c.a., posterior carotis cerebialis artery.
p.c.v., post-cerebral vein.
phx., pharynx.
pit., pituitary.
p.m., pila metoptica.
pmax., premaxilla.
post.cop., posterior copula.
p.p., pila prootica.
p.p.g., pre-profundus ganglion.
p.p.pl., pre-profundus placode.
p.preop., pila preoptica.
pr.a., processus ascendens.
p.q.c., pterygo-quadrato cartilage.
preart., prearticular.
preocc.a., pre-occipital arch.
preor.g., pre-oral gut.
pr.ot., processus oticus.
pr.pt., processus pterygoideus.
pteryg., pterygoid.
pv., prevomer.

r.alv.VII(fac.), ramus alveolaris facialis.
r.bucc.VII, ramus buccalis facialis.
r.card.X, ramus cardiac X.
r.gast.X, ramus gastricus X.
r.h.fac., ramus hyomandibularis facialis.
r.hypobr., ramus hypobranchialis.
r.inmand.V, ramus intermandibularis V.
r.int.X, ramus intestinus X.
r.j.fac., ramus jugularis facialis.
r.mand.V, ramus mandibularis V.
r.mand.e.fac., ramus mandibularis externus facialis.
r.mand.Vmass., mandibularis V branch to masseter.
r.max.V, ramus maxillaris V.
r.mentalis V, ramus mentalis V.
r.ment.e.fac., ramus mentalis externus facialis.

r.ment.i.fac., ramus mentalis internus facialis.
r.nas.i.V, ramus nasalis internus V.
r.o.p.V, ramus ophthalmicus profundus V.
r.o.p. V br. I, II, ramus ophthalmicus profundus branch I and II.
r.oti., ramus oticus.
r.pal.VII, ramus palatinus facialis.
r.ph.IX, ramus pharyngeus IX.
r.ptrem.X, ramus post-trematicus X.
r.rec.int.X, ramus recurrens intestinalis X.
r.rec.lar.X, ramus recurrens laryngeus X.
rud.ga.sp.n.I, rudimentary ganglion spinal nerve I.
rud.v.som.I, rudimentary ventral somite I.

s.o.fac., superior ophthalmicus facialis.
sol.n.(nas.), solum nasi.
som. II, III, somite II, and III.
sp., spiracle.
sp.ch., spinal cord.
sp.ga.n.I, II, spinal ganglion nerve I, and II.
sp.n. I, II, III, spinal nerve I, II, III.
sp.n. I, d.r., spinal nerve I, dorsal root.
sp.n. I, v.r., spinal nerve I, ventral root.
sp.n. II, d.r., spinal nerve II, dorsal root.
sp.n. II, v.r., spinal nerve II, ventral root.
sq., squamosal.

t.c., trabecula cranii.
temp., temporalis muscle.
thorhy., thoracohyoideus muscle.
t.horn., trabecular horn.
t.infraorb., truncus infraorbitalis.
t.m.p., taenia marginalis posterior.
trach., trachea.
trans.vent., transversus ventralis muscle.
trap., trapezius muscle.
tr.n., trochlear nerve.
tym., tympanic pouch.

v.br.n. I, II, III, IV, V, VI, VII, vagus branchial nerves I-VII.
v.c.l., vena capitis lateralis.
v.c.m., vena capitis medialis.
v.hypobr.anast., vago-hypobranchial anastomosis.
v.ph. I, II, III, vagus pharyngeus I, II, III.
v.pretrem. I, II, III, vagus pretrematicus I, II, III.
v.p.trem. I, II, III, vagus post-trematicus I, II, III.
v.ram.sp.n. I, II, ventral ramus spinal nerve I, II.

PLATE 1.

PLATE 1.

Photomicrographs all transverse sections.

15 mm. stage.

- Fig. 1. Pre-profundus placode.
- Fig. 2. Part of the r. ophthalmicus profundus nerve.
- Fig. 3. Part of the facialis ganglion and the spiracular pouch.
- Fig. 4. Small ganglion and dorsal root to spinal nerve I.

19 mm. stage.

- Fig. 5. Pre-profundus ganglion and nasal sac.
- Fig. 6. R. maxillaris V joining the r. buccalis facialis.
- Fig. 7. Origin of the r. buccalis facialis from the lateralis VII ganglion, and the relation of the latter to the gasserian ganglion.
- Fig. 8. Origin of the r. hyomandibularis facialis from the facialis ganglion.
- Fig. 9. Origin of the vagus branchial nerve I from ganglion X.
- Fig. 10. Origin of the hypoglossal (spino-occipital) nerve from medulla.



PLATE 2.

PLATE 2.

Photomicrographs all transverse sections.

26 mm. stage.

- Fig. 1. Deep profundus V and the origin of the palatine branch of the r. ophthalmicus profundus V.
- Fig. 2. Origin of the oculomotor nerve from the ventro-lateral margin of the mesencephalon.
- Fig. 3. Region just posterior to the eyeball.
- Fig. 4. Origin of the r. mandibularis V. The gasserian and anterior facial ganglia and various cartilaginous structures are seen.
- Fig. 5. Origin of the r. palatinus VII.
- Fig. 6. The r. hyomandibularis facialis separated from the facialis ganglion by the anterior basicapsular commissure.

30 mm. stage.

- Fig. 7. Structures in the nasal sac region.
- Fig. 8. Origin of the r. oticus ?
- Fig. 9. Origin of the r. alveolaris facialis and r. jugularis facialis.
- Fig. 10. Emergence of the r. hypoglossus via the hypoglossal foramen.
- Fig. 11. General picture in the region of neural arch I.

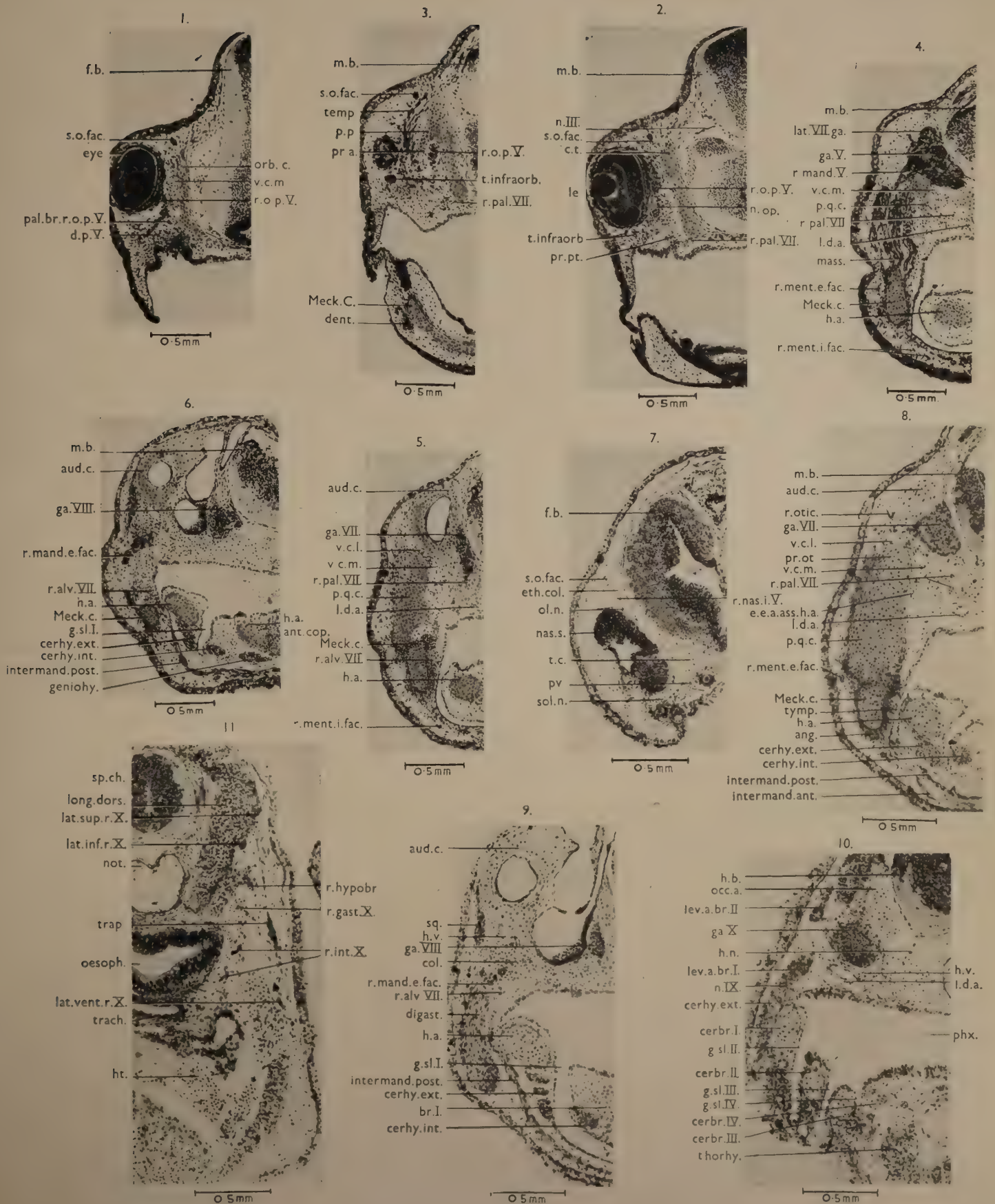


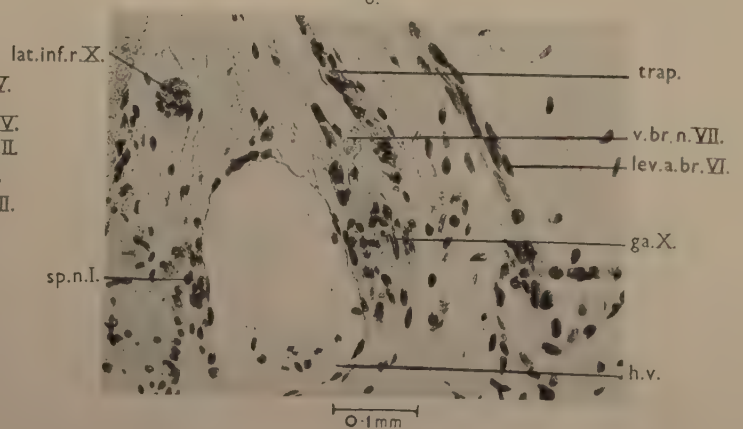
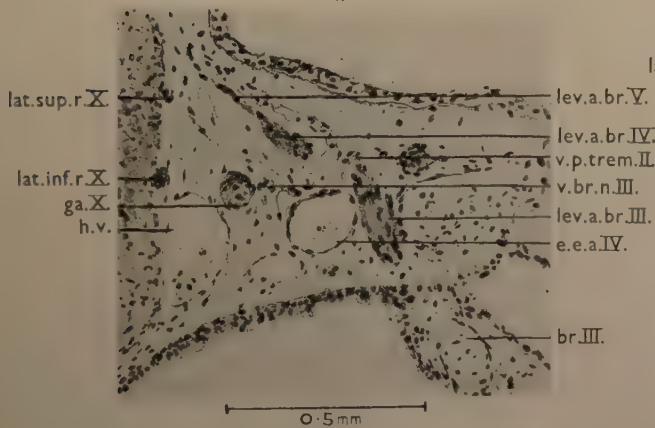
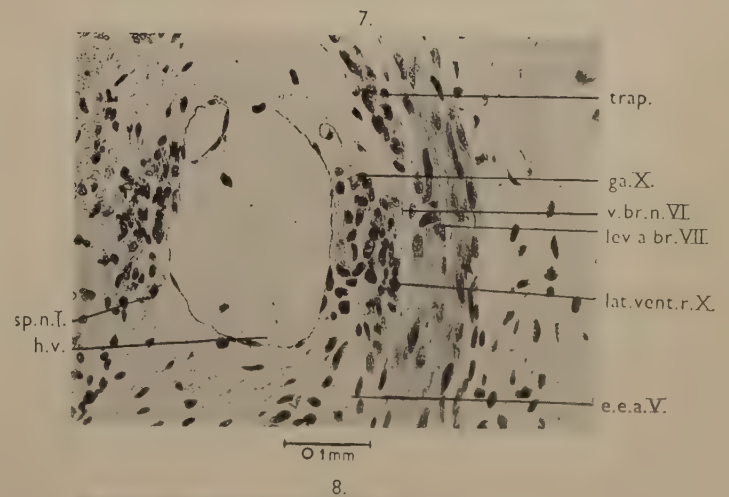
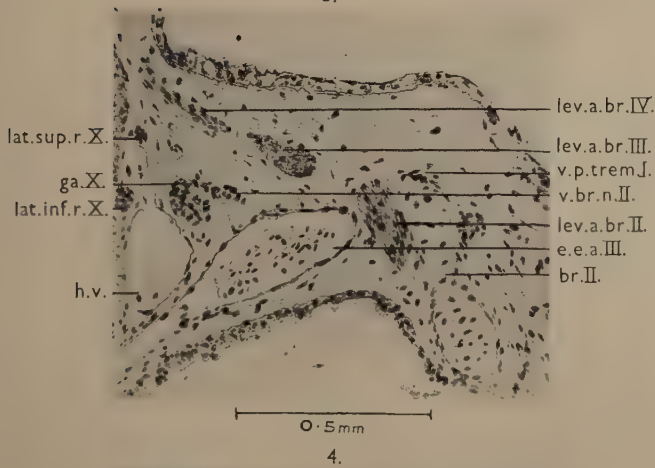
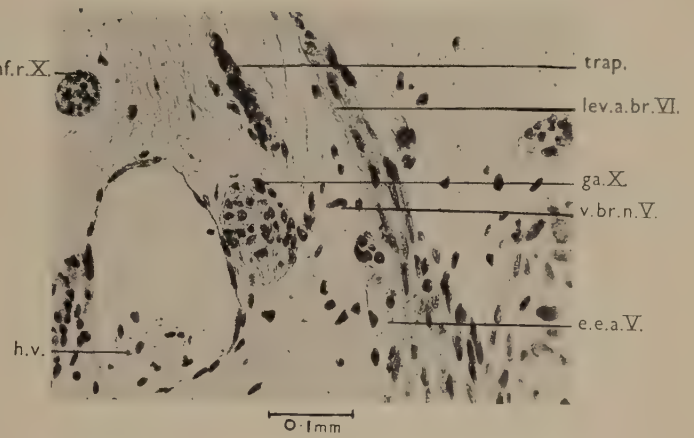
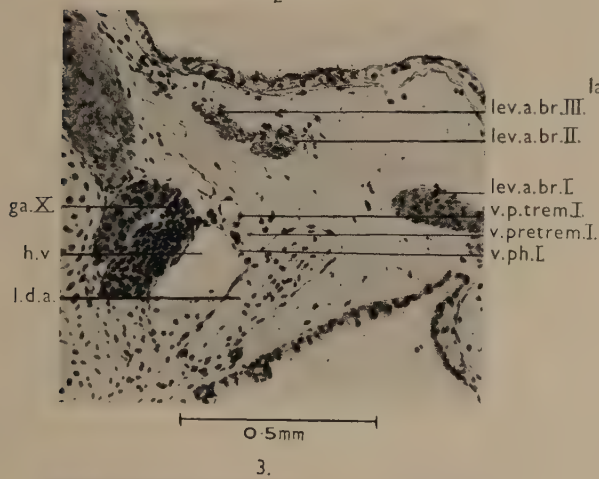
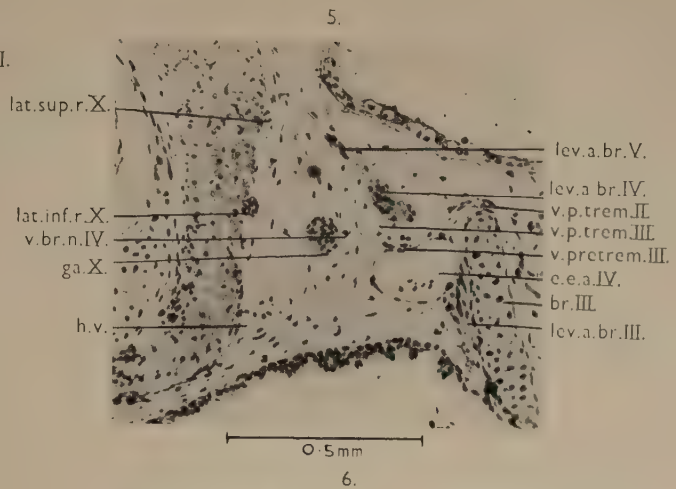
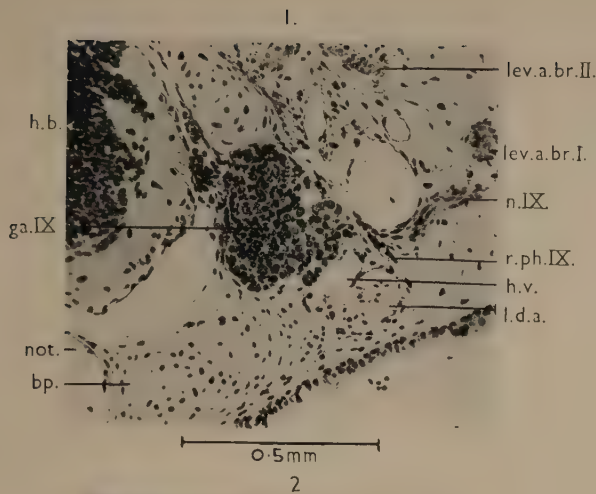
PLATE 3.

PLATE 3.

Photomicrographs all transverse sections.

32 mm. stage.

- Fig. 1. Glossopharyngeal nerve.
- Fig. 2. Vagus branchial nerve I.
- Fig. 3. Vagus branchial nerve II.
- Fig. 4. Vagus branchial nerve III.
- Fig. 5. Vagus branchial nerve IV.
- Fig. 6. Vagus branchial nerve V.
- Fig. 7. Vagus branchial nerve VI.
- Fig. 8. Vagus branchial nerve VII.



The experimental analysis of feather pattern in the
Amherst Pheasant, *Chrysolophus amherstiae* (Leadbeater).

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(With Plates 1 and 2 and 17 figures in the text.)

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I. THE MORPHOLOGICAL BASIS OF FEATHER PATTERNS.

Introduction.

The pattern of a definitive feather is the result of a series of processes which take place in the developing feather germ and which have their final expression in a number of features in the completed, keratinized feather. The principal of these features are:—the shape and final size of the feather, and the nature and distribution of its colour. Experimental studies during the last forty years have shown that in some birds the developmental processes taking place in the feathers may be markedly influenced by factors external to the feather germ, of which the most important are the secretions of the gonads and certain other endocrine glands.

In the present investigation on the plumage of the Amherst Pheasant *Chrysolophus amherstiae* (Leadbeater) an attempt has been made to describe, in detail,

the feather pattern in the normal bird and later to follow the changes in morphogenesis induced in male soma feathers grown in varying hormonal environments. The plumage of the Amherst Pheasant is well suited to this type of analysis since there are marked differences in a number of characters between feathers of comparable tracts on the normal male and female. In both the male and female birds the feathers of each tract are distinct from those of neighbouring tracts. In previous work on the effect of sex hormones on plumage observations have been largely confined to changes in the growth rate, pigmentation and shape of the feather. In the present study it has been found that, in addition to these features, the following are of great importance in the development of pattern—the final size of the feather, its barring pattern and the structure of the median barbules.

The principles of feather development were laid down at the end of the last century in the works of Davies (1889) and Strong (1902). In general, Davies' observations on the development of nestling and definitive contour feathers in the pigeon have formed the basis of nearly all subsequent accounts, and there is now little doubt that they were essentially correct. More recently, however, a new theory of feather development has been put forward by Lillie and his co-workers at Chicago. The investigation (Lillie & Juhn, 1932) which formed the basis of this theory followed the postulation by Juhn, Faulkner & Gustavson (1931) of a threshold in the response of feather follicles to endocrine secretions and of the dependence of this threshold on the growth rate of the feathers. The main point at issue in this controversy lies in the different interpretation of the method whereby the feather shaft is formed. Davies (1889) stated that the shaft was formed in the feather germ from a thickening of its dorsal wall, and that the barb rudiments became attached to this shaft rudiment at their proximal ends. According to Lillie & Juhn (1932) the feather shaft is formed by the concrescence of the two halves of the "collar", a new term denoting the ring of *stratum malpighi* cells proximal in the feather germ to the barb ridges. They postulated that as the collar tissues of the two sides grew together, the primary barb ridges were carried dorsally and distally by what they termed tangential movement. This theory has been severely, but justifiably, criticized by Hosker (1936) and 'Espinasse (1939) who have particularly emphasized that ridge formation is a relatively passive process, and that there is no evidence for a movement of cells, such as might take place if the two halves of the collar were to fuse in the mid-dorsal line.

Lillie & Juhn (1938) and Lillie (1942) have now modified their views on the origin of the shaft in development. From their (1938) paper it appears that they now admit that the central part of the shaft is formed in accordance with the classical theory, but they still insist that concrescence plays a part in the formation of the lateral surfaces of the shaft. Further work on the subject is contained in three papers on development analysis of plumage by Juhn & Fraps (1936) and Fraps & Juhn (1936 a, b). In the second paper of this series they define an isochrone (a term originally introduced by Hardesty, 1933) as "the locus of points of simultaneous and identical reaction or determination in homologous reactive centers of the germ". This is a useful concept and is referred to in the present analysis of feather pattern in *Chrysolophus*.

Colours in feathers.

The constituent colours of a feather pattern may be divided into two groups according to whether they are due to chemical pigments alone (pigmentary colours) or to the presence in the same feather of a chemical pigment and of a structure in the barbs or barbules which may greatly affect the colour of the feather when seen in incident light (structural colours).

Melanins are the most widespread of the pigmentary colours found in birds and they occur in feathers in a number of different colours ranging from yellow through red brown to black. Spöttel (1914) and Görnitz (1923) investigated melanins from the feathers of many species of birds. On the basis of their solubility in alkali, they recognized a paler, more soluble group of melanins. Further critical work on the solubility of different types of feather melanins has been done by Frank (1939).

Melanins may be deposited in all parts of the feather, but in a study of patterns it is mainly their distribution in the barbs and, more particularly, the barbules, which is of importance. In the barbs melanin granules are usually deposited in medullary cells, although they occasionally occur in the sheath layer. In the barbules melanin may be distributed uniformly, in which case other colour factors, such as structure or carotenoid pigments, do not enter into the production of the final coloration. In iridescent feathers melanin pigmentation occurs in the same barbules as the iridescent structure. In some cases there may be a special arrangement of the melanin, for instance in grey feathers melanin is usually deposited distally in the barbules (see below, the results of Experiments C 5 and C 7).

Some of the yellow and red colours of feathers are due to the presence of carotenoid pigments, usually deposited in the barbs. Desselberger (1930) has described the process of carotenoid deposition round small globules of fat in the tissues of developing feathers. Carotenoid pigments were not found in the feathers studied in the present work.

Bogdanow (1858) was the first to distinguish clearly between pigmentary and structural colours in feathers, and Fatio (1866) later recognized the two different types of structural colour in feathers, namely those shown by iridescent feathers and those of blue or green non-metallic feathers. The work of Haecker (1890), Haecker & Mayer (1902), Kniesche (1914) and Mason (1923) has shown that the structures essential for the reflection of blue light from a barb surface are a turbid porous layer composed of transparent keratin with a refractive index of 1.52 and air filled spaces with a refractive index of 1.0003, overlying a deposition of melanin granules. The exact origin and shape of the air spaces forming the turbid layer is not clear, but Rayleigh (1871) showed that when white light rays strike such a combination of two transparent bodies of different optical densities, the resultant diffuse reflection will consist mainly of blue rays. Feathers showing blue structure are common among the pigeons and many other birds, but were not found in the Amherst Pheasant. Iridescent feathers, on the other hand, are very common in the pheasants, and Mason (1923) has shown that they are interference colours of thin films, of the type seen in soap bubbles and films of oil on water.

Iridescent barbules differ from non-iridescent barbules in lacking most of the hooks and also in many cases the long thin pennulum. In a normal non-iridescent feather the barbules are orientated with reference to the feather vane so that only their dorsal edges are directed upwards towards the observer, that is, they are arranged like the leaves in a book. In such cases the relatively thin visible part of the barbule cannot play an important part in the production of optical effects. In iridescent feathers, on the other hand, the barbule becomes twisted (at its base or more distally) through an angle of 90 degrees, so that its broad (originally proximal) side comes to be directed upwards. This results in a greater area of the heavy melanin deposition being visible from above, and in addition, transverse sections show that the keratin of the flattened barbules is laid down in the form of laminae (Elsässer, 1925).

The adult plumages of the Amherst Pheasant.

The plumage of the Amherst Pheasant has been described in general terms by Gould (1850-83) but his account is inadequate for present purposes since he gives no details of feather size, iridescence or barbule characters. The following account of the plumage of the pendent, back and saddle tracts of the normal male and female is intended to form a basis for the experimental observations.

The patterns of the feathers in each tract are described with particular reference to the coloration of the feather, whether by pigment or structure, and to the incidence of barring patterns. The feathers of each tract are further characterized by measurements of the final length of the feather (table 1) and of the lengths and widths of the median barbules.

TABLE 1.

Feather lengths (in millimetres) in normal male and female Amherst Pheasants.

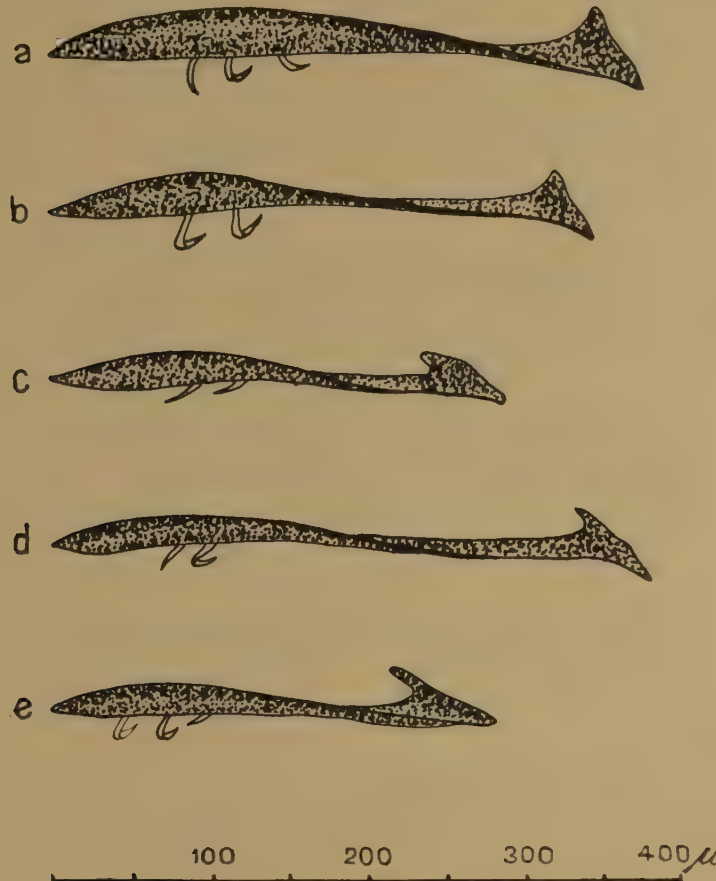
Tract	No.	Male		No.	Female	
		Mean	Range		Mean	Range
Pendent	9	98.1	89-102	11	28.2	24-33
Back	15	73.1	65-86	18	64.9	60-70
Saddle	15	75.7	73-78	13	70.2	64-74

Particular attention has been paid to the characteristics of the median barbules since these structures are primarily concerned in the coloration and pattern of the feathers. In particular, the median barbules are the seat of the iridescent colours. In every case a group of twenty neighbouring barbules was measured, and the mean taken. Barbules in the neighbourhood of the shaft are usually smaller and less typical than those in the remainder of the vane, and therefore each group of twenty barbules was measured at a standard distance (1.2 mm.) from the edge of the shaft, in the middle of the bar or other feature of which they were the sample.

In a normal non-iridescent feather each median barbule presents its thin dorsal edge to the observer looking at the dorsal (or upper) surface of the feather, while its sides are facing the neighbouring barbules. In such cases it is the apparent width (or thin edge) which has been measured and which plays a part in the colour

characteristics of the feather. In an iridescent feather, on the other hand, torsion has taken place at or near the base of the median barbules, so that the originally proximal side faces upwards. The width measured in this case, besides being the apparent width, is also the true width. From the pattern viewpoint it is the apparent width only which is the operative width, but from the morphological

Fig. 1.

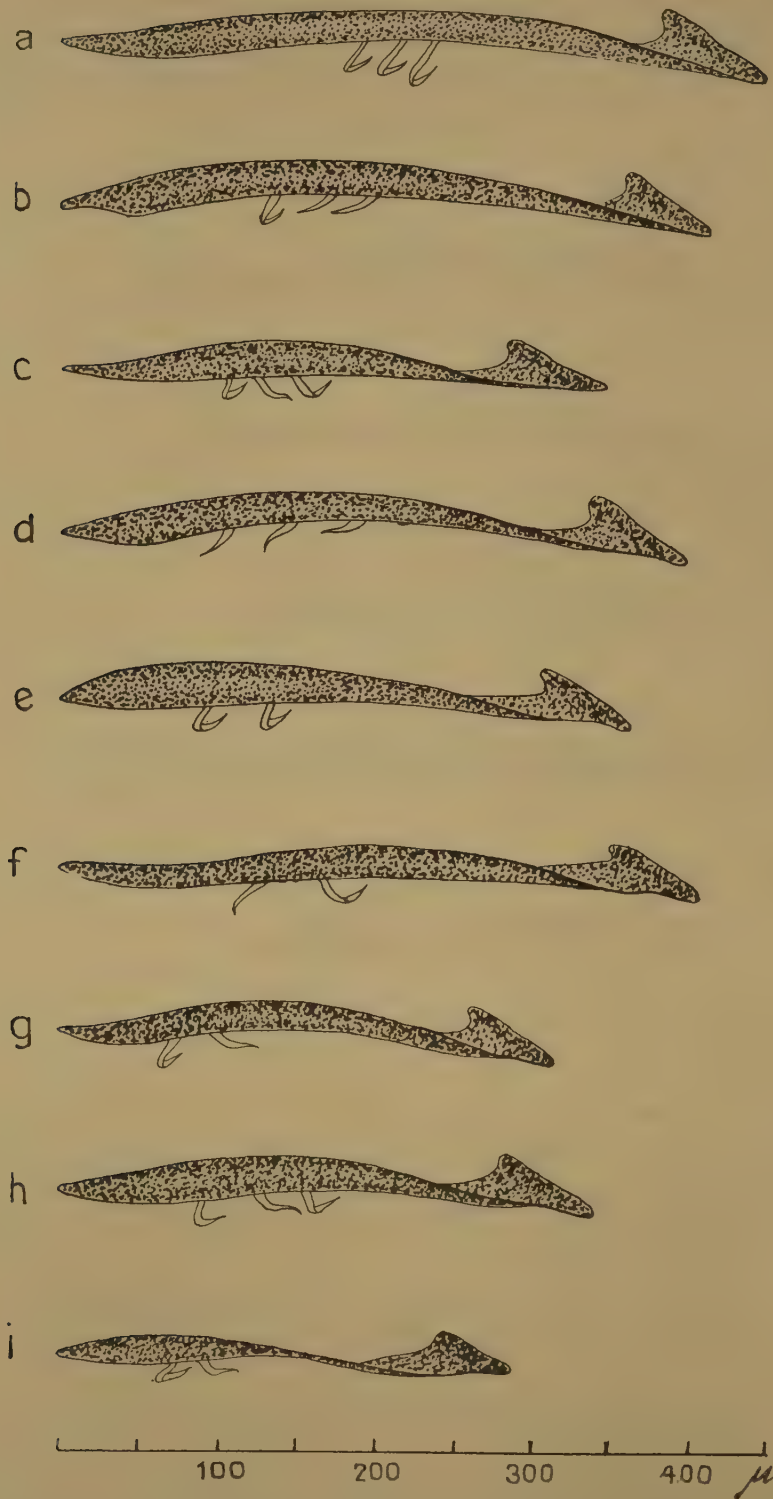


Pendent tract median barbules.

- a.* White barbules from area between the two iridescent dark green bars. Normal male.
- b.* White barbules from area proximal to subterminal iridescent dark green bar. Normal male.
- c.* Iridescent grey barbule, from feather of a male which had received three injections, each 200 γ oestrone.
- d.* Light brown barbule. Overlap zone of subterminal bar. Male with 100 γ oestrone per day.
- e.* Light brown barbule. Overlap zone near subterminal bar. Male with 100 γ oestrone per day.

point of view some distinction must be made between barbules whose apparent width is also their true width and those in which it is not. In some barbules torsion only affects the distal half of the barbule (distal torsion), while in a few cases torsion takes place about one-third of the length from the barbule base so that the middle third presents its broad side to the observer ; in such cases further

Fig. 2.

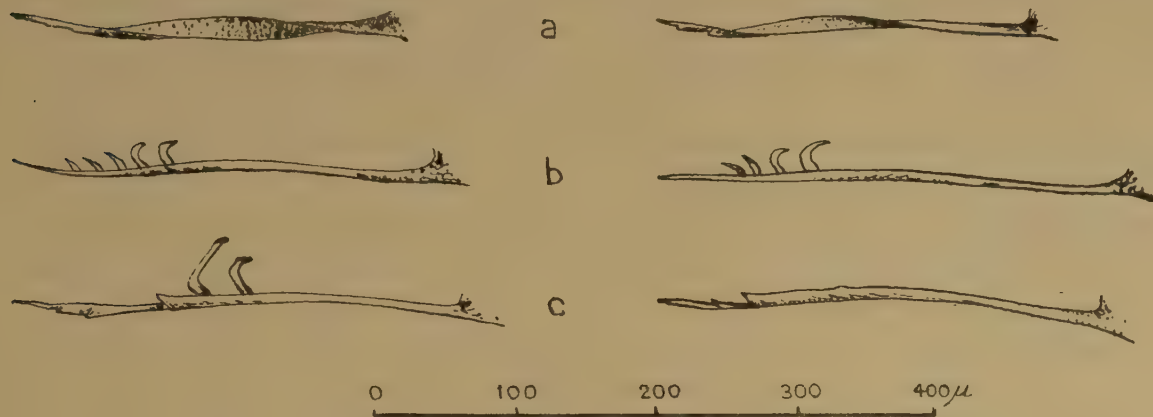


Pendent tract, median barbules of the subterminal iridescent dark green bar.

- a.* Normal male. *b.* Male with 10 γ oestrone. *c.* Male with 50 γ oestrone. *d.* Male with 100 γ oestrone. *e.* Male with 270 γ oestradiol. *f.* Male with 100 γ stilboestrol. *g.* Male with 500 γ testosterone propionate. *h.* Male with 7000 γ testosterone dipropionate. *i.* Normal female.

torsion occurs distal to the middle third so that the distal third has in fact been twisted through 180° and now presents its narrow, originally lower or ventral edge, to the observer (text-fig. 3 *a*).

Fig. 3.



Back tract median barbules, from dark brown and light brown bars.

a. From male receiving 2.5 γ oestrone per day.

b. From male receiving 100 γ oestrone per day.

c. From normal female.

TABLE 2.

Linear measurements (in μ) of median barbules

(means of 20 measurements).

a. NORMAL MALE FEATHERS.

Tract	Bar or pattern feature	Mean length	Mean width	Torsion
Pendent	Terminal iridescent dark green bar	551	26	T
	Subterminal iridescent dark green bar	425	19	T
	White vane proximal to subterminal bar	320	14	DT
Back	Iridescent dark green vane	448	24	T
Saddle	Terminal yellow zone	278	7	A
	Iridescent dark brown area	243	22	T
	Non-iridescent dark brown area	299	10	A

b. NORMAL FEMALE FEATHERS.

Pendent	Terminal iridescent dark grey brown bar	185	11	T & DT
	Subterminal iridescent dark grey brown bar	265	11	T & DT
	Distal light brown bar	224	8	A
	Dark brown vane	257	6	A
	Proximal light brown bars	260	6	A
Back	Dark brown bars	361	7	A
	Light brown bars	344	6	A
Saddle	Dark brown flecks	384	6	A
	Light brown areas	399	6	A

These distinctions are given in the last column of table 2 by the following symbols, which are used in the descriptions of the experimental feathers :—

- T denoting torsion at or near the base of the barbule. The width measurements refer to the true width.
- DT denoting torsion of the distal part of the barbule only. The width measurements refer to the true width of this distal portion.
- MT denoting torsion affecting the middle third of the barbule length, the distal third being thin and tapering. The width measurements refer to the true width of the middle portion.
- A denoting absence of torsion and iridescence. The width measurements refer to the apparent width of the thickest part of the barbule.

The means and ranges of the feather lengths in normal male and female feathers are given in table 1.

The normal male feathers.

Pendent (Pl. 1, fig. 1). The feather is long and spatulate in shape, the vane is pure white crossed by (i) a terminal narrow crescentic iridescent dark green bar, with a proximal edging of a lighter tint, and (ii) a subterminal straight iridescent bar similarly coloured.

The iridescent dark-green barbules are twisted at their base so that their wide flat *sides* face upwards towards the observer (text-fig. 2 *a*). The structure of the white parts of the vane is of some interest. When viewed in reflected light these parts are not iridescent, but they do show a slight surface reflection giving a shiny effect to the feather. Examination of the white median barbules showed that in the area between the two iridescent dark green bars the white median barbules are twisted at their bases (text-fig. 1 *a*), while in the white area proximal to the subterminal bar distal torsion occurs (text-fig. 1 *b*). The barbule structure in the white area of the vane is therefore similar to that of the iridescent dark green barbules, but having no background of melanin pigmentation it does not show iridescence. Such a background can, however, be provided artificially by staining these feathers for two days in picronigrosin or bismarck brown, or for three days in Weigert's lithium haematoxylin. When this was done the vane showed slight iridescence.

Back (Pl. 1, fig. 7). The feather is bright iridescent dark green, with a narrow velvety black fringe at the tip, but with no other barring or pattern. The iridescent barbules are heavily pigmented with black melanin.

Saddle (Pl. 1, fig. 13). The vane consists of a terminal yellow band, followed by a partly iridescent dark brown area, which is crossed by a single incomplete bar of white or pale yellow. The proximal two-thirds of the feather are made up entirely of silky grey down barbs. The terminal yellow bands shows two distinct zones, an outer one without barbules followed by an inner zone with normal barbules. The distal part of the dark brown area is iridescent while the proximal part is non-iridescent, the pigmentation in both being melanin. In the incomplete white and yellow bar the median barbules are similar in size and structure to the non-iridescent dark brown barbules, but they are not pigmented by melanin.

The normal female feathers.

Pendent (Pl. 1, fig. 6). The feather is short and oval in shape. The terminal bar of the vane is dark grey brown with slight iridescence and is separated from a similar subterminal bar by a non-iridescent light brown bar. Proximal to the subterminal bar the vane is non-iridescent dark brown crossed by one or two light brown bars.

Back (Pl. 1, fig. 12). The feather vane consists of alternate dark and light brown bars, pigmented by melanin. The angle between these bars and the shaft is acute proximally. There is no iridescence and none of the median barbules show torsion (text-fig. 3).

Saddle (Pl. 1, fig. 17). The distal two-fifths of the vane are coloured light brown with dark brown flecks which are arranged in three or four indistinct dark bands, better developed in some feathers than in others. The most proximal of these dark bands gives place rather abruptly to the down barbs which occupy the remainder of the vane.

Growth curves of normal feathers.

Growth curves of developing feathers have been recorded by Krizenecky (1930) and by Juhn, Faulkner & Gustavson (1931). The following details of feather growth are intended to show the difference between the growth curves of the three tracts in normal male and female Amherst Pheasants; they also form a basis for further discussion of growth rate modification in the experimental feathers.

Regenerating feathers were mapped out in each tract, so that every feather could be identified individually. Each feather was then measured twice a week during the period of regeneration. The measurements were started as soon as the feather germs appeared above the surface of the skin, usually about ten days after plucking. The mean was taken of a number of measurements in each tract and the growth curves plotted from these means are shown in text-figs. 9, 12 and 15. The following points of interest arise.

Pendent tract. In the female the feathers of this tract grow at a slower absolute rate than those of the male, and the period of growth is much shorter (thirty-eight days in the female, sixty-six days in the male). The completed female feather is, therefore, shorter in length (text-fig. 9).

Back tract. The female feathers grow slightly faster than the male during the first thirty-five days but slower from then until completion of growth at fifty-two days. The male feathers grow for a longer period (fifty-nine days) and reach a greater length (text-fig. 12).

Saddle tract. The female feathers again grow slightly faster than the male during the first part of the growth period but they grow for a shorter period (thirty-eight days in the female, forty-eight in the male), and the completed male feather is a little longer than that of the female (text-fig. 15).

During the main part of their growth the curves of the three male feathers are very similar, the back and saddle feathers grow a little slower than the pendent during the first twenty-five to thirty days of growth, but after that they grow a little faster. The growth period and the final size of the pendent feathers are both longer than in the back and saddle.

In the female the growth curves of the back and saddle feathers are similar, but the female pendent feathers grow much slower.

Further discussion on the growth curves of the normal feathers is reserved until later, when consideration is also given to the determination of final size.

II. SEXUAL DIMORPHIC PLUMAGE IN *CHRYSOLOPHUS*.

Introduction.

The relation between the gonads and sexual dimorphic plumage in gallinaceous birds has been investigated by a number of workers in the United States, France, Britain and elsewhere. Goodale (1913) showed that castrated Brown Leghorn hens assumed a male type of plumage. Other important works are those of Pézard (1918), Zawadowsky (1922), Caridroit (1926), Domm (1924, 1927), Greenwood (1928), and Benoit (1929).

From these investigations which involved orchidectomy, ovariectomy and cross-transplantation of gonad tissue it was concluded that in fowls the male, capon and poulard all carry a "neutral" plumage, whose development is inhibited in the normal female by the ovarian secretions. In subsequent work Freud, de Jongh & Laqueur (1929) obtained feminization of the plumage of Brown and Golden Leghorn cocks and capons following injections of ovarian extracts. These results have been repeatedly confirmed, using injections of pure female sex hormones. In the Leghorn races the feathers studied did not show any barring, but in other races of fowls with barred feathers Emmens & Parkes (1940) found that oestrogen injections into capons induced the female type of barring. Blivaiss (1947) used different doses of oestrogen in thyroidectomized roosters but there are no detailed records of the comparative effects on feather structure and pattern of different doses of oestrogen injected throughout the feather growth period into normal sexually dimorphic birds.

The apparent completeness of sex reversal in the hen following bilateral ovariectomy and the observation of "feminized" plumage in the cock with an ovarian implant led Zawadowsky (1928) to postulate an equipotentiality of the two sexes as regards plumage. Later work on a greater number of species, has, however, shown that, at any rate in pheasants, the male and female do not show equipotentiality in the development of plumage characteristics. Finlay (1925) noticed certain differences between the sexes in Brown Leghorn fowls, which are not conditioned by the gonads, e.g. size, spurs, and the presence of an oviduct in females only, but regarded the plumage as equipotential in the two sexes. Kopec & Greenwood (1930) working on the effect of yolk injections on Brown Leghorns obtained changes in the colour and pattern in the direction of femaleness, but not complete feminization of shape.

The pheasants show the most marked sexual dimorphism of all gallinaceous birds, and Champy (1935) found that, in general, they react in a similar way to fowls when castrated or when injected with ovarian extracts. Danforth (1937 a, b), however, noticed that in certain pheasants the so-called female type plumage of a

cock or capon undergoing oestrogenic hormone injections was quite distinct from the normal female plumage of the species. In much of his work Danforth made use of skin transplantation as a means of analysing plumage characteristics. This method is particularly valuable since it allows the reactivity of feather follicles of one sex to be tested in the hormone environment of the opposite sex without causing any disturbance of the endocrine system.

In races of the Common Fowl skin grafted from one race to the opposite sex of another race produced feathers showing the race characteristics of the donor, while the sexual type was in accordance with the host sex (Danforth, 1929; Danforth & Foster, 1929). However, there are races of fowl in which ovarian secretions play no part in the control of the sexually dimorphic plumage. Montalenti (1934) found that in Barred Plymouth Rocks there are slight differences in reactivity between the feather follicles of the two sexes. In this race sexual dimorphism affects the width of the white bars, and is quite independent of the sex hormones. In this case the gene for white barring probably acts quantitatively, the male, with two such genes, having wider white bars and therefore appearing brighter in colour.

In Reeve's Pheasants Danforth (1937 a) found that male skin transplanted to a male host, and female skin transplanted to a female host, produced normal male and female feathers respectively. But male skin on a female host and female skin growing on a male host produces new type feathers differing from one another, being in many respects intermediate between the normal male and female types. These experiments and similar ones on the Common Pheasant (Danforth, 1937 b) showed clearly that the feather follicles of male and female pheasants are not equipotential and that male skin does not react to female sex hormones in the same way as skin from a female host. The difference in reactivity is probably under the control of genetic factors.

In general, therefore, oestrogenic substances exert an inhibiting action on the feather coloration of normal and caponized male gallinaceous birds, but there is considerable variation in the characters affected, and in some cases at least, the genetic constitution of the feather follicle cells plays an important part in determining the exact nature of the response.

Experiments on the plumage of male Amherst Pheasants.

(a) Sex hormone injections.

The following experiments were designed to determine the effect of varying doses of natural and synthetic sex hormones on feather morphogenesis in the male Amherst Pheasant.

In each bird used a number of feathers was plucked from the three experimental tracts (pendent, back and saddle), and daily (or less frequent) intramuscular injections of hormone were started at the same time. The regenerating feathers were mapped out when the feather germs appeared above the surface of the skin, which usually occurred about nine to ten days after plucking. Each of these feathers, which could be identified individually, was measured throughout its

growth. The injections and measurements were continued until all the experimental feathers in the three tracts had reached their full size. Table 3 gives a synopsis of the treatment given to the experimental birds.

TABLE 3.

Amherst Pheasant.

Summary of experiments on plumage using injections of various oestrogens and androgens.

Experiment	Sex	Injection of :	Period of feather growth	Period of injection
B 7	♂	Nil (Control bird)	23/10 to 17/2 1937	
C 5	♂	2.5 γ oestrone daily	1/10 to 6/12 1938	1/10 to 6/12 1938
C 7	♂	5 γ oestrone daily	1/10 to 9/12 1938	1/10 to 9/12 1938
B 2	♂	10 γ oestrone daily	23/10 to 17/12 1937	23/10 to 17/12 1937
B 3	♂	50 γ oestrone daily	23/10 to 10/12 1937	23/10 to 10/12 1937
C 98	♂	100 γ oestrone daily	1/10 to 29/11 1938	1/10 to 29/11 1938
H 1	♂	270 γ oestradiol dipropionate daily	9/2 to 26/3 1940	9/2 to 26/3 1940
F 7	♂	100 γ stilboestrol daily	21/1 to 11/3 1939	21/1 to 11/3 1939
G 2	♂	100 γ oestrone daily (1st half)	19/10 to 19/12 1939	19/10 to 6/11 1939
G 1	♂	100 γ oestrone daily (2nd half)	19/10 to 19/12 1939	7/11 to 19/12 1939
C 98 a	♂	Nil " After effect " of C 98 injections	29/11 to 14/2 1939	
B 4	♂	500 γ testosterone propionate every 2nd day	23/10 to 11/12 1937	23/10 to 11/12 1937
J 3	♂	7000 γ testosterone dipropionate daily	23/2 to 3/4 1940	26/2 to 3/4 1940
K 1	♂	200 γ oestrone (3 doses only)	14/2 to 15/4 1939	On 9, 10 & 11 March 1939
D 6	♀	Nil (Control bird)	8/1 to 15/2 1938	

The detailed descriptions of feather coloration and pattern and the measurements of the median barbules are recorded in Vever (1949). The experimental work was carried out in the Department of Zoology and Comparative Anatomy, Oxford, during tenure of the Christopher Welch Scholarship in Biology, 1938-40, and I am indebted to Prof. J. Z. Young, F.R.S., for much helpful criticism and advice during this period. The analysis of the feathers produced has been done at the Plymouth Laboratory since the war, and I am indebted to Mr. F. S. Russell, F.R.S., for his interest in the work. The oestrone and oestradiol were kindly supplied by Prof. S. Zuckerman, F.R.S., who has also helped in many

other ways, and the testosterone dipropionate by Prof. V. Korenchevsky. For the stilboestrol I am indebted to Prof. Sir Robert Robinson, F.R.S. These hormones were in each case dissolved in arachis nut oil. The testosterone propionate was supplied by Messrs. Ciba under the trade name Perandren.

(b) *Skin transplantation experiments.*

Ten Amherst chicks were used, of which eight survived the transplantation operation. All the chicks were hatched on 25th June 1938, and the operations were carried out on 28th June. It is not possible to determine the sex accurately at this early age and so cross-transplants were made between random pairs. After anaesthetization with ether a piece of skin approximately 2.0 cm. by 1.5 cm. was removed from the back-saddle area of each chick and transplanted to the other member of the pair where it was sewn in position with fine surgical silk. The details of the operation followed the methods described by Danforth & Foster (1929).

Each piece of skin was taken from an area on the dorsal surface of the chick corresponding with the posterior part of the back tract and the anterior part of the saddle tract. The eight chicks which survived the operation were reared normally over the winter of 1938-39 and the grafts were examined again in May 1939. By then it was possible to sex each host bird, and the grafts were found to have been made as follows :—

- Bird C Male skin (from Bird D) growing on a male host.
- Bird D Male skin (from Bird C) growing on a male host.
- Bird E Male skin (from Bird F) growing on a female host.
- Bird F Female skin (from Bird E) growing on a male host.
- Bird G Male skin (from Bird H) growing on a female host.
- Bird H The graft (from Bird G) did not grow on its male host.
- Bird J Female skin (from bird K) growing on a female host.
- Bird K Female skin (from Bird J) growing on a female host.

Birds C and D. Male skin graft on a male host.

The healed borders of the grafts persisted and allowed the graft area to be distinguished from the surrounding host skin. In both birds the feathers of the graft were otherwise indistinguishable from those of the host. Each piece of grafted skin showed normal male back feathers in the anterior part, followed by normal male saddle feathers in the posterior part.

Birds J and K. Female skin graft on a female host.

The donor feathers were of the normal female back and saddle type, having the same pattern and coloration as the surrounding host feathers.

Birds E and G. Male skin graft on a female host (Pl. 2, figs. 29 and 33).

Both these grafts healed successfully, but very few donor feathers were produced on Bird E. In Bird G a number of back and saddle feathers were produced. The back feathers of this graft were similar in coloration and pattern to the back feathers grown on the male soma in the presence of oestrogenic hormones, in

particular, those with the injections of 50 γ oestrone (Experiment B 3) and 270 γ oestradiol dipropionate (Experiment H 1). The barbules of the light brown and dark brown bars were of the non-iridescent type. The angles made by the brown bars with the shaft were also similar to those in Experiments B 3 and H 1.

The saddle feathers of this graft were barred with dark and light brown and buff, the most distal dark brown bar showing iridescence. Here again the saddle feathers showed a similar pattern to those of Experiments B 3 and H 1 and of the other experiments in which oestrogenic substances were injected into the male, and they were quite distinct in pattern from normal female saddle feathers growing on the skin surrounding the graft.

Bird F. Female skin graft on a male host (Pl. 2, fig. 28).

The anterior part of this graft grew successfully and healed with a normal edge to the surrounding male skin. In the posterior part, however, the donor skin became detached and had to be cut off from the healthy anterior portion. As a result none of the female saddle skin survived to produce feathers and only a few feathers were produced from the donor female back tract skin. These feathers were darkly pigmented like the normal male back feathers but showed no iridescence and the vane was marked by a few small patches of light brown melanin pigmentation.

Transplantation of skin between pendent tracts of different birds was not attempted as there is no way of preventing the chicks from removing the graft from the back of the neck before it is healed.

Modification of final size, pigmentation and barbule structure in the experimental feathers.

(a) *In the pendent tract.*

The changes induced in the feathers of the pendent tract grown on the male body under the influence of varying doses of natural and synthetic hormones are perhaps the most striking in the present investigation. In addition to the wide differences in coloration and pattern between the normal male and female feathers, there are also very marked differences in their final size and shape, and in the form of their barbules. These characters have all been modified, in varying degrees, in the experimental feathers.

The Oestrone series. Pendent feathers regenerated under the influence of the two smallest doses of oestrone (2.5 γ and 5 γ per day) show little significant change in size or shape, and they retain the white and iridescent dark green areas characteristic of the normal male. However, the dark green bars (Pl. 1, fig. 2) are no longer so clearly marked off from the pure white vane, and there is a spread of melanin pigmentation over the vane proximal to the subterminal bar. In the same feathers comparison of the lengths and widths of the median barbules in the subterminal iridescent bar shows that there is no significant difference between them and those of the same bar in the normal male (table 4). Throughout the discussion on this tract comparisons will be made between the measurements

(lengths and *true* widths) of the barbules of the subterminal iridescent bar, this being one of the only features in the pendent tract which is present in some form in all the experimental feathers as well as in the normal male and female feathers.

TABLE 4.

Amherst Pheasant—Pendent Tract.

Shaft and median barbule measurements.

Experiment *	mm.	μ		μ		μ		μ		μ	
	Shaft	Terminal		Subterminal		Grey		Dark		Light	
	length	iridescent		iridescent		iridescent		brown		brown	
		bar		bar		vane		vane		vane	
		L	W	L	W	L	W	L	W	L	W
♂ Normal	98	551	26	425	19						
♂ + 2.5 γ oestrone	93	491	21	374	21	242	12				
♂ + 5 γ oestrone	92	510	19	428	19						
♂ + 10 γ oestrone	69	502	22	376	18	215	14				
♂ + 50 γ oestrone	37	373	19	325	13	284	13	317	6	311	7
♂ + 100 γ oestrone	54	508	20	343	14	339	18	278	7	241	7
♂ + 270 γ oestradiol dipropionate	31			351	15	241	12	284	9	282	8
♂ + 100 γ stilboestrol	37	349	15	391	18			272	10	319	12
♂ + 500 γ testosterone propionate	37	397	20	274	16	324	11	300	8		
♂ + 7000 γ testosterone dipropionate	34	420	20	282	16	321	14	314	6	275	8
♀ Normal	28	185	11	265	11			257	6	260	6

L = length of median barbules.

300=grey brown.

W = width of median barbules.

* See table 3 for further details of the experiments.

The pendent feather grown with 10 γ oestrone per day (Pl. 1, fig. 3) is still spatulate in shape, but considerably shorter. Proximal to the subterminal bar it is coloured smoky grey, being iridescent in the distal part of this area. The same feather also shows two slight traces of light brown in the proximal half of the vane. The median barbules of the sub-terminal bar are shorter than in the normal male (text-fig. 2 *b*).

With the next dose (50 γ oestrone per day) the feather is short, broadly spatulate in shape and has no pure white in the vane (Pl. 1, fig. 4). The area between the terminal and subterminal bars is iridescent blue grey, and the subterminal bar grades off proximally into dark grey brown which covers most of the remainder. In four patches, however, light brown melanin has been deposited, but without forming definite bars across the vane. The subterminal barbules (text-fig. 2 *c*) are shorter and narrower, and the iridescence is less pronounced than in the preceding feathers.

In the pendent feather grown with 100 γ oestrone per day (Pl. 1, fig. 5) the coloration and pattern show features of great interest. The shape of the vane is similar to that of the normal male. The length is considerably shorter than in

the normal male but rather longer than in the preceding feather. This is an unexpected result since the previous feathers have shown a decrease in length with increased oestrone dosage. However the bird on which the present feathers were grown may possibly have differed from the others in its general reactivity to oestrone since there is also a discrepancy in the barbule measurements consonant with the discrepancy in shaft length. The lengths and widths of the subterminal barbules (text-fig. 2 *d*) are intermediate between those of the two preceding feathers ($\text{♂ bird} + 10 \gamma$ and $\text{♂ bird} + 50 \gamma$ oestrone). In general, therefore, the feathers grown with 50γ oestrone per day show considerably more "feminization" than those grown with 100γ oestrone.

In the pendent feather grown on the male bird with injections of 100γ oestrone per day (Pl. 1, fig. 5) the vane proximal to the subterminal bar is iridescent blue grey grading to non-iridescent grey brown. Just distal to and partly overlapping the subterminal dark green bar there is a light brown bar extending across the whole vane. This bar is set at a different angle to the shaft from the subterminal bar and this accounts for the region of overlap. Proximal to the subterminal bar there are three other light brown bars, and the angle between them and the shaft is acute distally. The main interest in this feather lies in the overlapping of the subterminal with the most distal light brown bar. Quite clearly the pigmentation isochrone for the light brown bar is set at a different angle in the feather germ from the pigmentation isochrone for the subterminal iridescent bar. Furthermore, although the pigmentation of the barbules in the overlap region is light brown induced by the oestrone injections, the median barbules thus pigmented still retain the structure typical of the iridescent dark green barbules of the non-overlapped parts of the subterminal bar (text-fig. 1 *d*). Similarly the median barbules of those parts of the distal light brown bar not overlapped by the subterminal bar also have a structure comparable with that of iridescent median barbules (text-fig. 1 *e*). The *true* width of the median barbules in both these adjoining areas of light brown is 12μ and they differ considerably in structure from the median barbules of the proximal light brown bars, which have an *apparent* width of 7μ .

These facts suggest that the distal area of the pendent feather is one in which the structural characteristics associated with the two iridescent bars are very persistent. In the presence of oestrone the median barbules of the subterminal bar are only reduced in size without the loss of their characteristic structure, even when light brown pigment is deposited. This persistence of the iridescent type of median barbules also appears in the area between the terminal and subterminal bars (see text-fig. 1 *e*).

For the purposes of this discussion the normal female feather (already described) may be considered as belonging to the oestrone series. In this feather both terminal and subterminal bars are present and show some iridescence.

Reference to table 4 shows that in those feathers of the oestrone series which show iridescent grey areas, the median barbules of such areas are typically broad. Dark and light brown bars occur in only two of the experiments ($\text{♂ bird} + 50 \gamma$ and $\text{♂ bird} + 100 \gamma$ oestrone per day) and their median barbules are of the narrow type characteristic of similar bars in the normal female.

So far in this discussion no attempt has been made to correlate the reduction in pendent shaft length with the reduction in length and width of the median barbules of the subterminal bar. It is, however, likely, *a priori*, that as the size of the feather shaft and barbs decreases the size of the barbules will also decrease. In text-fig. 5 the shaft lengths of the feathers are plotted against the mean lengths and widths of the median barbules of their subterminal bars. There is a decrease in both sets of measurements with an increase in oestrone dosage. This graph also shows the apparently discrepant position of the feather grown on the male receiving 100 γ oestrone per day. The correlation between the lengths and true widths of the median barbules of the subterminal bar is shown in text-fig. 4.

The action of oestrone on the morphogenesis of the pendent feather in the male may be summarized as follows :—

(i) Final size—there is a reduction in the final size of the feather with increase in dosage of oestrone.

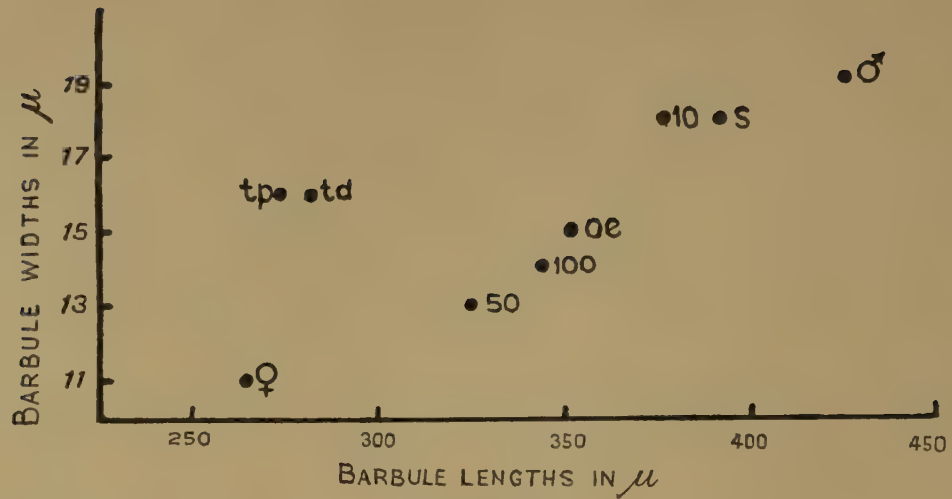
(ii) General shape—there is a fairly well-marked change from the spatulate male shape to the ovoid female shape with increased dosage of oestrone.

(iii) Coloration—pigmentation is by melanin in all the feathers. In the male feathers and in those of the male treated with small doses of oestrone only dark brown melanin is deposited. In the female feathers and in those of the male treated with larger doses of oestrone, light brown and dark brown melanin are deposited. Structural (iridescent) colours are well developed in the male feathers, but occur in reduced form in the female. Feathers grown on the male undergoing oestrone injections show a reduction in degree of iridescence with increased dosage of the hormone, this reduction being closely correlated with a reduction in the size, particularly the width, of the median barbules (see further below under (v)).

(iv) Barring pattern—barring is of two types. Firstly, in the male there are two well developed iridescent dark green bars. These bars are present in reduced form in the female. Administration of oestrone to the male causes considerable reduction in the absolute sizes of these bars; this modification increases with increased dosage and is associated with the reduction in size of the barbules in these bars. Secondly, in the female feathers and in those of the male treated with large doses of oestrone there are light brown bars set at a different angle to the shaft from the two iridescent bars. Where these two types of barring overlap the pigmentation is conditioned by oestrone, while the median barbules retain the structure characteristic of iridescent barbules.

(v) Barbule structure—the typical broad iridescent barbules of the subterminal bar are reduced in length and width in the presence of oestrone (text-fig. 2). This reduction is correlated approximately with increasing oestrone dosage. In the area of the vane proximal to the subterminal bar the barbules of the male are pure white, with distal torsion of the median barbules. With low doses of oestrone these median barbule tips become pigmented with dark brown melanin giving an iridescent grey colour. With larger doses the iridescent structure is lost, the

Fig. 4.

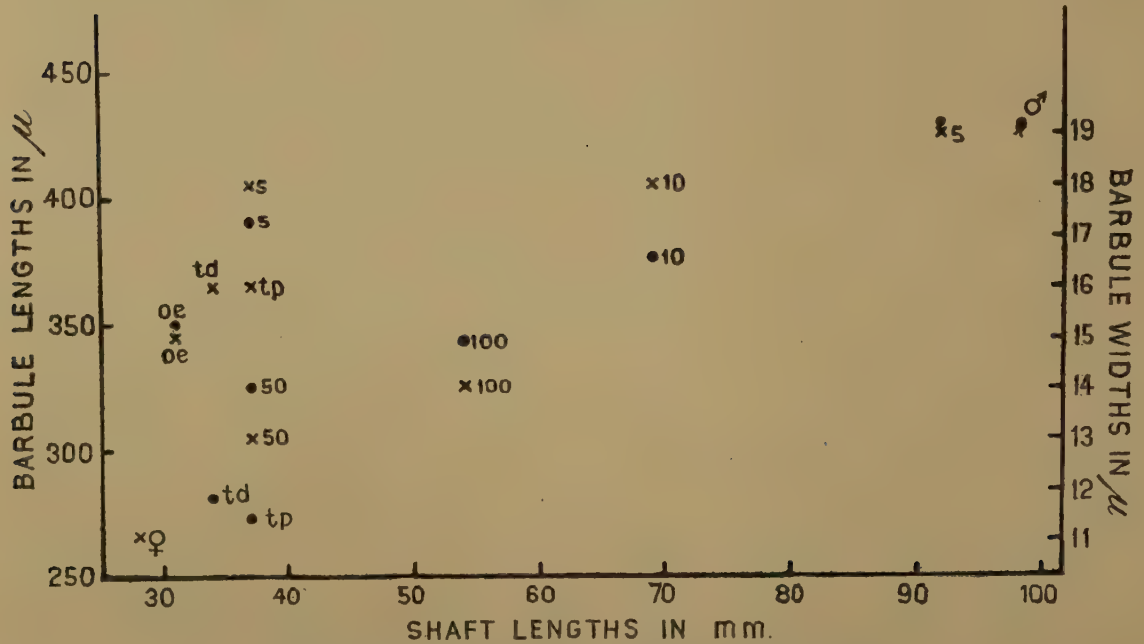


Pendent tract.

Subterminal iridescent dark green bar.

Barbule widths plotted against barbule lengths. (Symbols as in text-fig. 5.)

Fig. 5.



Pendent tract. Subterminal iridescent dark green bar.

Barbule lengths and widths plotted against shaft length.

Figures denote daily dosage of oestrone in γ .

s = stilboestrol injection. oe = oestradiol injection. tp = testosterone propionate injection.

td = testosterone dipropionate injection.

● barbule lengths. × barbule widths. ♂ normal male. ♀ normal female.

median barbules becoming long and thin without torsion, and being pigmented with either dark or light brown melanin, give non-iridescent dark or light brown colours.

Other oestrone feathers. Four further experiments involved the administration of oestrone during only a part of the feather regeneration period.

In the first of these experiments Bird C 98 was used. Immediately after the feathers grown on this bird under treatment with 100 γ oestrone had been plucked, the succeeding feather generation was allowed to grow without further administration of hormone. Under these circumstances the high concentration of oestrone remaining in the blood after the previous experiment influenced the morphogenesis of the new feathers until the hormone was gradually and finally eliminated. The pendent feathers grown in this way (Pl. 2, fig. 18) show modifications in their distal parts comparable to those produced in the previous feather generation while oestrone was being administered. They are medium-sized and narrow spatulate in form, with quite well-developed terminal and subterminal bars. Between these two bars the vane is iridescent smoky grey crossed by a single light brown bar. In a few of the feathers there is overlapping of the subterminal bar by the light brown bar with results similar to those found in the feathers of the previous generation. Proximal to the subterminal bar the vane is again smoky grey, with slight iridescence for about 6 mm., and it is crossed by an incomplete light brown bar. The remainder of the feather is white. This experiment shows clearly the events taking place in a feather grown with a gradually diminishing concentration of oestrone.

In the second and third experiments large daily injections (each 100 γ) of oestrone were given during the first and second halves of the feather regeneration period respectively. As would be expected the feathers regenerated with the injections at the beginning of the growth period (Pl. 2, fig. 19) show oestrone modified feathers in the distal part of the vane. The terminal and subterminal bars persist with reduced iridescence, and the rest of the vane is smoky grey with slight iridescence, crossed by two incomplete light brown bars.

In the feathers grown without injections for the first half and with a heavy dose of oestrone during the second half of the regeneration period (Pl. 2, fig. 20), the distal part of the vane is the same as in the normal male, while the proximal part is smoky grey with slight iridescence, but without trace of light brown bars. It is interesting to note that the grey vane is very faintly patterned by bars of lighter grey (almost white). This induced grey and white barring is the result of fluctuations in the concentration of oestrone in the body and is particularly noticeable during the first part of the injection period. The frequency of these bars on the vane is much greater than that of the light brown bars induced in feathers with a steady dose of 100 γ oestrone throughout growth (Experiment C 98). Furthermore the angle made by these grey and white bars with the shaft is different from the angle made with the shaft by the non-iridescent dark and light brown bars in Experiment C 98.

This type of grey and white barring is again shown in the fourth experiment of this series (Experiment K 1). Normal growth was allowed to proceed until

the subterminal bar and the first part of the proximal white vane had been formed. Then three large doses of oestrone (each 200 γ) were given on three successive days. These injections were registered on the vane as a broad iridescent grey band (Pl. 2, fig. 22). Proximal to this band the vane continues to be grey for some time as the concentration of oestrone in the body gradually falls. Even the injection of 600 γ oestrone spread over three days has not provided a concentration in the blood sufficient to inhibit completely the iridescent grey median barbules or to induce the dark or light brown colorations with their associated non-iridescent barbule structure.

Oestradiol and Stilboestrol Injections. Pendent feathers grown under the influence of a daily injection of 270 γ of oestradiol dipropionate (Experiment H 1) are shown in Pl. 2, fig. 21; they are small and similar in shape to the normal female type. In coloration and pattern they are similar to those grown with 50 γ and 100 γ oestrone per day. A plot of subterminal barbule lengths against width (text-fig. 4) confirms this general macroscopic similarity.

The feathers grown with 100 γ stilboestrol per day (Experiment F 7) are rather large and more spatulate (Pl. 2, fig. 23) than the oestradiol feathers. In coloration and barring they are similar to the feathers grown with 100 γ oestrone, and they also show an exactly comparable overlapping of the distal light brown bar with the subterminal bar. A plot of the subterminal barbule lengths against widths (text-fig. 4) gives a point along the straight line of the oestrone series readings, close to that for the feather grown with 10 γ oestrone. Using such a strong synthetic oestrogen as stilboestrol it might be expected that greater modification of the barbule lengths and widths would have taken place, and that the reduction in barbule size would have been correlated more closely with the reduction in shaft length. Plots of subterminal median barbule lengths and widths against shaft length (text-fig. 5) shows that, relative to the points of the oestrone series, stilboestrol induces more response in the shaft length than in the barbule size. To a lesser degree this is also true of the oestradiol feathers.

Testosterone injections. Emmens & Parkes (1940) found that only the capons of henny breeds of fowl (e.g. Silver Campine) responded to testosterone by feminization of plumage. In the capons of normal breeds (e.g. Brown Leghorn) large doses of testosterone only produced symptoms which were referable to thyroid deficiency.

In the Amherst Pheasant male hormones were found to produce some features in the feathers similar to those produced with natural and synthetic oestrogens.

Injections of a relatively low dose of testosterone propionate (500 γ every second day) (Experiment B 4) gave a short spatulate feather with iridescent terminal and subterminal bars. Between these bars the vane is white with some grey and proximal to the subterminal bar it is dark grey with slight iridescence distally. There is no trace of light brown pigmentation. With an injection of 7,000 γ per day of testosterone dipropionate (Experiment J 3) the feathers are again short and spatulate, and distally the pattern is similar to that in the feathers of the preceding experiment, except that the area between the terminal and subterminal bars is now all grey (Pl. 2, fig. 25). Proximally the vane is again iridescent dark

grey, but it is now crossed by a single light brown bar with traces of a second bar more proximally.

A plot of the subterminal barbule lengths of these two experimental feathers against their shaft lengths (text-fig. 5) gives points which are close to the straight line of the oestrone series. From this it appears that the two testosterone esters induce a shortening of the median barbules approximately proportional to the reduction in shaft length. However, a plot of barbule widths against shaft length (text-fig. 4) gives two points which are well off the straight line of the oestrone series. It is clear that the action of the testosterone esters on barbule structure is different in degree from that of oestrone; the testosterone esters, whether directly or indirectly, reduce shaft length and barbule length in the same way as oestrone, but not the barbule widths.

Comparison of text-figs. 4 and 5 shows that in the pendent tract :—

(1) With oestrone, modification of shaft length, and subterminal barbule length and width is approximately proportional to the dosage.

(2) Injection of oestradiol dipropionate or stilboestrol does not modify barbule length or width to the same relative extent as shaft length. Modification of barbule length is, however, proportionate to the modification of barbule width.

(3) Injection of the two testosterone esters does not modify barbule width to the same relative extent as barbule length or shaft length.

Rensch (1925 a) has suggested that there is a possible relation between iridescent structure and heavy melanin pigmentation. The present observations show that the iridescent dark green median barbules of the male pendent subterminal bar (text-fig. 2 a) are larger and show a greater reflecting surface than the pure white median barbules of the same feathers (text-fig. 1 b). This difference between pigmented and unpigmented barbules showing iridescent structure suggests that there might be some connection between the two processes of heavy pigmentation and the broadening of the barbules. Rensch considered that the broad iridescent barbules were the result of an abundance of pigment acting mechanically; he argued that as the barbule rudiments in the feather germ were not hollow, a heavy intake of pigment could be accommodated by an increase in the width and length of the barbules but not in their thickness as they were already close-packed in the ridges of the germ like the leaves of a book. This may account for the condition in heavily pigmented iridescent median barbules such as those of the pendent subterminal bar, but it does not explain the presence of distal torsion, giving a broad barbule tip, in unpigmented white barbules on the same feather. Similarly in the distal light brown bar of the male pendent feather grown with 100 γ oestrone per day the barbules retain their iridescent structure even though pigmentation is reduced. It appears, therefore, that distal torsion occurs in the median barbules of the distal part of the pendent feather even in the absence of heavy pigmentation, but that torsion moves towards the proximal end of the barbules as the amount of pigmentation increases.

The constant occurrence of iridescent barbule structure along certain isochrones in all pendent feathers is very noticeable. This iridescence is reduced in the presence of gynaecogenic and androgenic hormones, but never lost, even in the

female. It appears then that this feature is primarily conditioned by genetic factors in the feather germ cells. If this is so there is a significant spread of the action of these factors on each side of the main isochrone along which they exert their strongest effect, as there is no sharp dividing line between iridescent and non-iridescent areas in the pendent feathers of either sex. The action of these factors may build up distally to an iridescent bar, may reach a maximum, associated with strong melanin deposition, at the isochrone of the bar itself, and may then decrease in effect proximally.

(b) *In the back tract.*

The brightly iridescent dark green male feather of this tract is modified, in the presence of female hormones, to a non-iridescent dark brown feather regularly barred with light brown. There is no single character, such as the subterminal bar of the pendent tract, which is present in all the feathers—male, female and experimental.

TABLE 5.
Amherst Pheasant. Back Tract.
Shaft and Median Barbule Measurements.

Experiment	mm. Shaft length	μ Iridescent dark green vane		μ Dark brown vane		μ Light brown vane	
		L	W	L	W	L	W
♂ Normal	73	448	24				
♂ + 2.5 γ oestrone	78	327	22	301	12	286	12
♂ + 5 γ oestrone	71	382	17	375	10	373	11
♂ + 10 γ oestrone	62	326	20	274	7	270	6
♂ + 50 γ oestrone	65			349	7	368	8
♂ + 100 γ oestrone	68			357	6	375	6
♂ + 270 γ oestradiol dipropionate	70			353	11	363	8
♂ + 100 γ stilboestrol	70			348	8	380	8
♂ + 500 γ testosterone propionate	59	291	23				
♂ + 7000 γ testosterone dipropionate	69			376	7	376	8
♀ Normal	65			361	7	344	6

L = length of median barbules.

W = width of median barbules.

In the experiments with the three lowest doses of oestrone (2.5 γ , 5 γ , and 10 γ per day) the build-up of the hormone at the start of feather regeneration has been too slow to induce any macroscopic changes and the feathers retain their iridescent (male) tips (Pl. 1, figs. 8 and 9). Examination of the median barbules shows that there has been some modification, involving reduction in the length and width of the iridescent barbules (see table 5). The more proximal parts of these feathers and the whole vane in the remainder of the oestrone, oestradiol and stilboestrol series show no iridescence. This is a result of the loss of torsion in the median barbules of nearly all the dark and light brown barred feathers. In two of the

oestrone feathers (2.5 γ and 5 γ daily), however, the dark and light brown median barbules are still relatively wide as loss of torsion is not complete. The same occurs in the dark brown barbules of the oestradiol feathers.

In the back tract there is no marked size difference between the feathers of the two sexes. There is also no correlation between shaft length and barbule length.

In those dark brown median barbules which show no trace of torsion there is an approximate correlation between barbule length and oestrone dosage:—table 5 shows that there is an increase in dark brown barbule length with increased oestrone dosage.

In general the lengths and apparent widths of the light brown median barbules are similar to those of the dark brown barbules. The exception to this occurs in the oestradiol feathers where the dark brown median barbules are broad and show median torsion while the light brown barbules of the neighbouring bar are narrow and lack all signs of torsion. It is possible that there is a critical concentration of hormone in the blood at which torsion is lost in light brown barbules but not completely so in dark brown barbules.

The transplantation experiments involving back tract skin produced male genotype feathers growing on a female (Pl. 2, fig. 29) which showed patterns very similar to those of the feathers in the oestrone and oestradiol series. In Bird F a few female genotype feathers were produced successfully on a male host. Under these conditions the female genotype feathers were similar in pigmentation to the normal male feathers, but lacked the iridescence and showed a few small patches of light brown pigmentation (Pl. 2, fig. 28). This suggests that in this species the female feather germ may respond to the presence of the normal male hormones more readily than the male genotype, but the evidence is not conclusive. The male back feather only responds to very large concentrations of male hormone (testosterone dipropionate, Pl. 2, fig. 26).

The experimental male genotype back feathers show a different barring pattern from the normal female back feathers; this difference is discussed below.

(c) *In the saddle tract.*

The experimental feathers of this tract are all very varied in appearance. In general all the hormone injections, except the testosterone propionate and the two lowest doses of oestrone, inhibited the production of the yellow colour in the terminal band and also its distal fringe of barbule-free barbs. The yellow was replaced in this band by buff. The apparent widths of the buff median barbules showed no significant difference from those of the yellow barbules, except in the stilboestrol feathers where they are exceptionally wide (10 μ) (table 6).

A subterminal iridescent bar is present in all the experimental male genotype feathers and in the normal male. It is usually dark brown but in two oestrone experiments (10 γ and 100 γ per day) it is grey green (Pl. 1, figs. 15 and 16). The widths of the median barbules of this bar in the experimental feathers are smaller than in the normal male, while their lengths are all greater. In the testosterone dipropionate feathers (Pl. 2, fig. 27) there is very little trace of this iridescent bar when viewed macroscopically, but microscopic examination revealed a few definite

TABLE 6.

Amherst Pheasant—Saddle tract.

Shaft and median barbule measurements.

Experiment	mm. Shaft length	Terminal yellow, buff or orange-red band		Subterminal iridescent grey green or dark brown bar		Dark brown vane		Light brown, buff or yellow brown bar		Other bars	
		L	W	Colour	L	W	Colour	L	W	L	W
♂ Normal	76	278	7	y	243	22	db	299	10		
♂ + 2.5 γ oestrone	80	291	6	r	236	17	db	370	7		
♂ + 5 γ oestrone	69	315	6	y	340	17	db	425	5		
♂ + 10 γ oestrone	68	221	6	y b	339	10	gg	387	6		
♂ + 100 γ oestrone	64	220	5	b	342	15	gg	388	7		
♂ + 270 γ oestradiol	69	282	7	b	358	17	g	416	6		
♂ + 100 γ stilboestrol	70	295	10	b	361	17	g	419	6		
♂ + 500 γ testosterone propionate	73	321	8	r or y	311	11	g	415	7		
♂ + 7000 γ testosterone dipropionate	64	201	8	b	295*	14	db	391	6		
♀ Normal	70							384	6		

y = yellow.
r = red.
g = green.

or = orange red.
db = dark brown.

L = length of median barbules.

W = width of median barbules.

b = buff.

gg = grey green.

* This iridescent bar is represented by a few barbules only.

wide iridescent barbules with twisted bases. There is no trace of the iridescent bar in the normal female feather (Pl. 1, fig. 17).

Dark brown areas occur in all the normal and experimental feathers. Pigmentation is by melanin and the barbules in such areas do not show iridescent structure. In the experimental feathers the dark brown median barbules tend to become longer with increased dosage of hormone, but there is considerable variation from one experiment to the next. Dark brown barbule widths are significantly less in the experimental and normal female feathers than in the normal male.

Light brown, yellow brown or buff bars and mottling occur in the normal female and in most of the experimental saddle feathers (table 6). Such bars do not occur in the normal male. Pigmentation in all these bars is again by melanin. The median barbules of these bars are variable in length, although they are all relatively long; the measurements (table 6) suggest that barbule lengths increase with hormone dosage. The barbule widths are all "apparent" except in the light brown bar of the 2.5 γ oestrone feathers in which the barbules show median torsion.

In the transplant experiments in which male skin was grafted to female hosts (Pl. 2, fig. 33) the male genotype follicles produced feathers comparable to those from saddle tracts of male birds undergoing oestradiol or stilboestrol treatment.

Barring patterns in normal and experimental feathers.

There are three types of barring pattern in the male genotype feather tracts studied :—

- (i) The iridescent bars of the pendent feathers and the light brown bars of the experimental feathers of this tract.
- (ii) The iridescent bar (sometimes two bars) of the male saddle feathers, and the parallel non-iridescent dark brown, light brown and buff bars of the experimental feathers of this tract.
- (iii) The dark and light brown bars of the experimental feathers of the back tract.

Each type of barring responds in a different way to the presence of hormones.

(i) The iridescent bars of the pendent tract show their greatest development in the normal male, but they persist in reduced form in the female and in the feathers of the male undergoing hormone treatment. There are probably two processes involved in the production of these bars, one being the deposition of dark melanin along a well-defined pigmentation isochrone in the feather germ. The other is the process whereby the median barbules become twisted at their bases so that the originally posterior sides of each come to face upwards towards the observer.

This process of torsion, associated with a broadening of the surface area of the observed side occurs in reduced form in the remainder of the distal part of the male pendent feather, where the white median barbules show distal torsion. It has already been shown that there may be some causal connection between heavy melanin pigmentation and iridescent barbule structure, but that, at the same time, barbule torsion and broadening does occur in unpigmented and lightly pigmented barbules near to strongly iridescent pattern features.

Many of the pendent feathers show light brown bars when grown in a female hormone environment, and these bars are deposited along different isochrones from those of the iridescent bars.

(ii) The iridescent bar of the male saddle feathers does not occur in the female. It does, however, persist in reduced form in all the saddle feathers grown on the male in the presence of gynaenogenic and androgenic hormones, and in the transplant of male saddle skin to a female. In some of the experimental feathers the bar appeared to be divided into two, due to the interruption of the originally single bar by the deposition of a non-iridescent hormone-induced bar. This iridescent bar is, therefore, probably controlled by factors present in the male genotype skin only, but there is evidence that its production can be reduced and in some cases interrupted in the presence of sex hormones.

(iii) In the back tract the dark brown and light brown bars of the female and of the experimental feathers are induced by the gynaecogenic hormones and to a lesser extent by very large doses of androgenic hormone. Incomplete traces of these bars appeared on the vanes of the feathers grown on female back skin grafted on to a male. This suggests that the normal male hormonal environment may have a slight "feminizing" effect on female genotype back feathers, which may, therefore, be more sensitive to sterol derivatives than homologous male genotype feathers.

The production of these dark and light brown bars is thus controlled by phenotypic factors. There is a noticeable difference between the barring of the normal female and that of the experimental feathers of this tract, in the angle at which the brown bars meet the shaft. A projection of the distal part of the vane of the female and of some of the experimental feathers (text-figs. 6, 7 and 8) shows this difference clearly, and also the different angles at which the barbs join the shaft. In every case the angles referred to are the proximal angles made by the colour bars or the barbs with the shaft. These projections show that male genotype feathers have relatively high shaft/bar and shaft/barb angles whereas female genotype feathers have smaller shaft/bar and shaft/barb angles.

Both these angles play a part in the production of the barring patterns. One variable (the shaft/barb angle) can be rendered constant by artificially moving all the barbs until they are at right angles to the shaft. This was done by a simplification of the method described by Juhn & Fraps (1936). The shaft and the barbs of one side of the vane were immersed in molten paraffin (m.p. 45° C.) and a small piece of filter paper was introduced under the vane. With the help of a fine paint brush the barbs were moved so that they took up a position perpendicular to the shaft. The whole preparation was then removed from the paraffin. Setting of the barbs in this position took place immediately and gave the preparations photographed in Pl. 2, figs. 30, 31 and 32.

These figures show that when the barbs are at right angles to the shaft, the shaft/bar angles are very similar in the feathers of both genotypes. This suggests that the angle at which the colour bars cross the barbs in the original feathers*

* This angle cannot be accurately measured in the natural feathers owing to the varied curvature of the barbs.

Figs. 6-8.

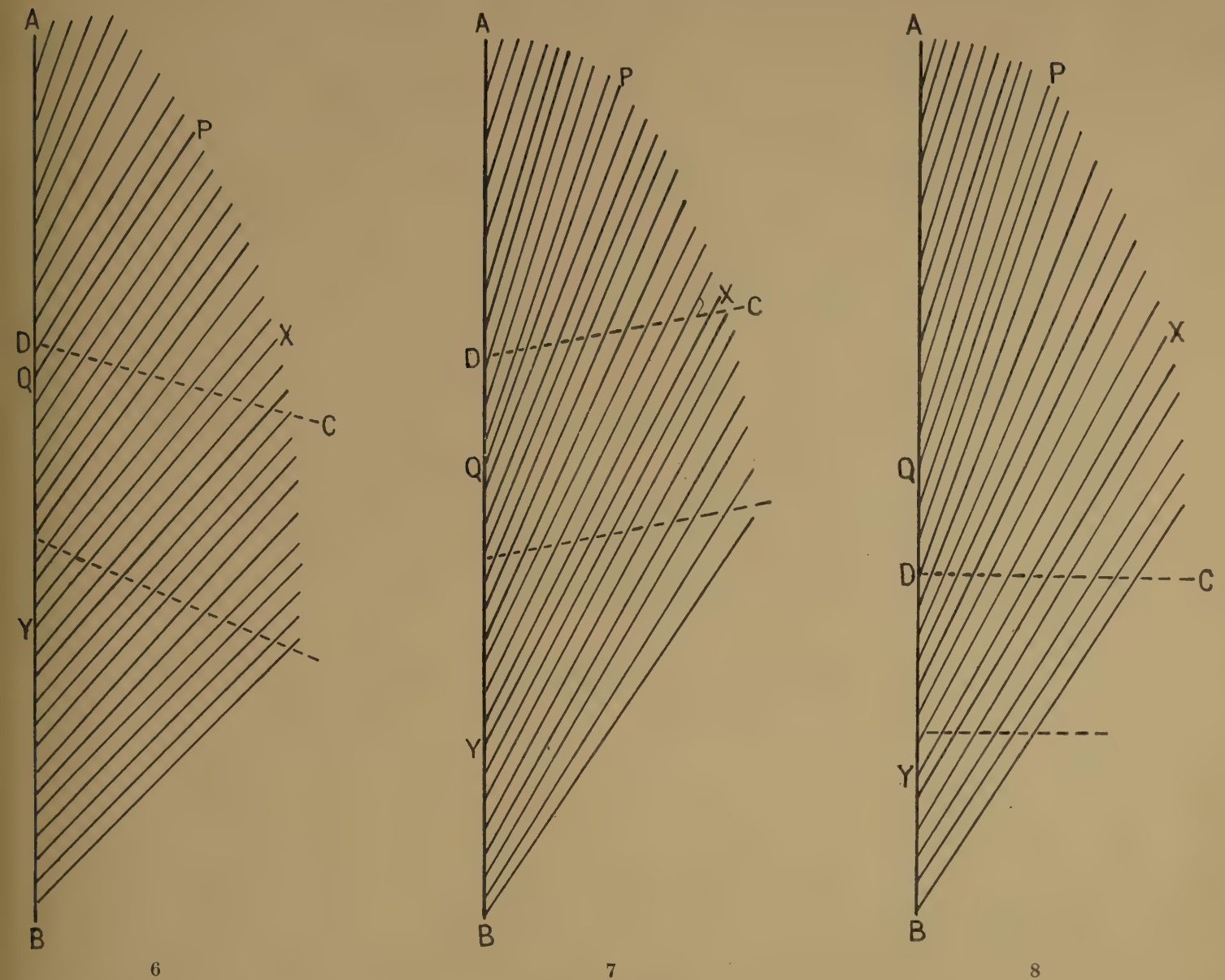


Fig. 6.—Back tract.

Projection of distal part of normal female feather. The barbs have been shortened. Dotted lines represent limits of a light brown bar.

Length $AB = 11.5$ mm. Angle $PQB = 147^\circ$. Angle $XYB = 140^\circ$. Angle $CDB = 75^\circ$.

Fig. 7.—Back tract.

Projection of distal part of male genotype feather grown with 270γ oestradiol per day. The barbs have been shortened. Dotted lines represent limits of a light brown bar.

Length $AB = 11.5$ mm. Angle $PQB = 160^\circ$. Angle $XYB = 156^\circ$. Angle $CDB = 101^\circ$.

Fig. 8.—Back tract.

Projection of distal part of male genotype feather grown with 100γ oestrone per day. The barbs have been shortened. Dotted lines represent limits of a light brown bar.

Length $AB = 11.5$ mm. Angle $PQB = 161^\circ$. Angle $XYB = 151^\circ$. Angle $CDB = 90^\circ$.

is the same in feathers of both genotypes, and that the difference in barring angles found in these feathers is largely due to the angle at which the barbs meet the shaft.

The difference between the shaft/barb angles of the two sexes may be partly due to differential setting of the barbs at the end of keratinization, the barbs in female genotype feathers becoming fixed at a wider angle than those of the male genotype. However it is considered that the main cause is to be sought earlier in development. The shaft/barb angles are, in fact, probably correlated with the angles at which the barb ridges of the early feather germ are formed relative to the shaft primordium. This suggestion should be examined in the course of any further work on this type of pattern analysis. There is, however, no doubt that the proximal shaft/barb angles of the male genotype back feathers never approached those shown by female genotype feathers, even when development took place in the presence of large doses of gynaecogenic hormones.

A comparison was also made of the widths of the light and dark brown bars in the back feathers of the two genotypes. In this analysis the most distal light brown (often mottled) bar and the first dark brown bar were not measured, as, in some of the experimental feathers this part of the feather still showed slight iridescence characteristic of the normal male feather. Measurements were, however, taken of the widths of the second light bar, the second dark bar, the third light bar and the third dark bar, and these are shown in table 7. These measurements do not indicate any significant difference in the width of the hormone-induced bars between male and female genotype feathers.

TABLE 7.

Width of dark brown and light brown bars in certain back feathers of the Amherst Pheasant.

(Measurements in millimetres, taken where the colour bars meet the shaft.)

		Second light bar	Second dark bar	Third light bar	Third dark bar	No. of feathers measured
Male with 50 γ oestrone	Mean	3.4	3.8	3.5	3.3	15
	Percentage	24.2	27.1	25.7	24.2	
Male with 270 γ oestradiol	Mean	3.3	4.8	3.0	4.7	20
	Percentage	21.0	30.1	18.8	30.0	
Female normal	Mean	2.7	4.3	3.0	4.0	20
	Percentage	19.3	30.7	21.4	28.6	

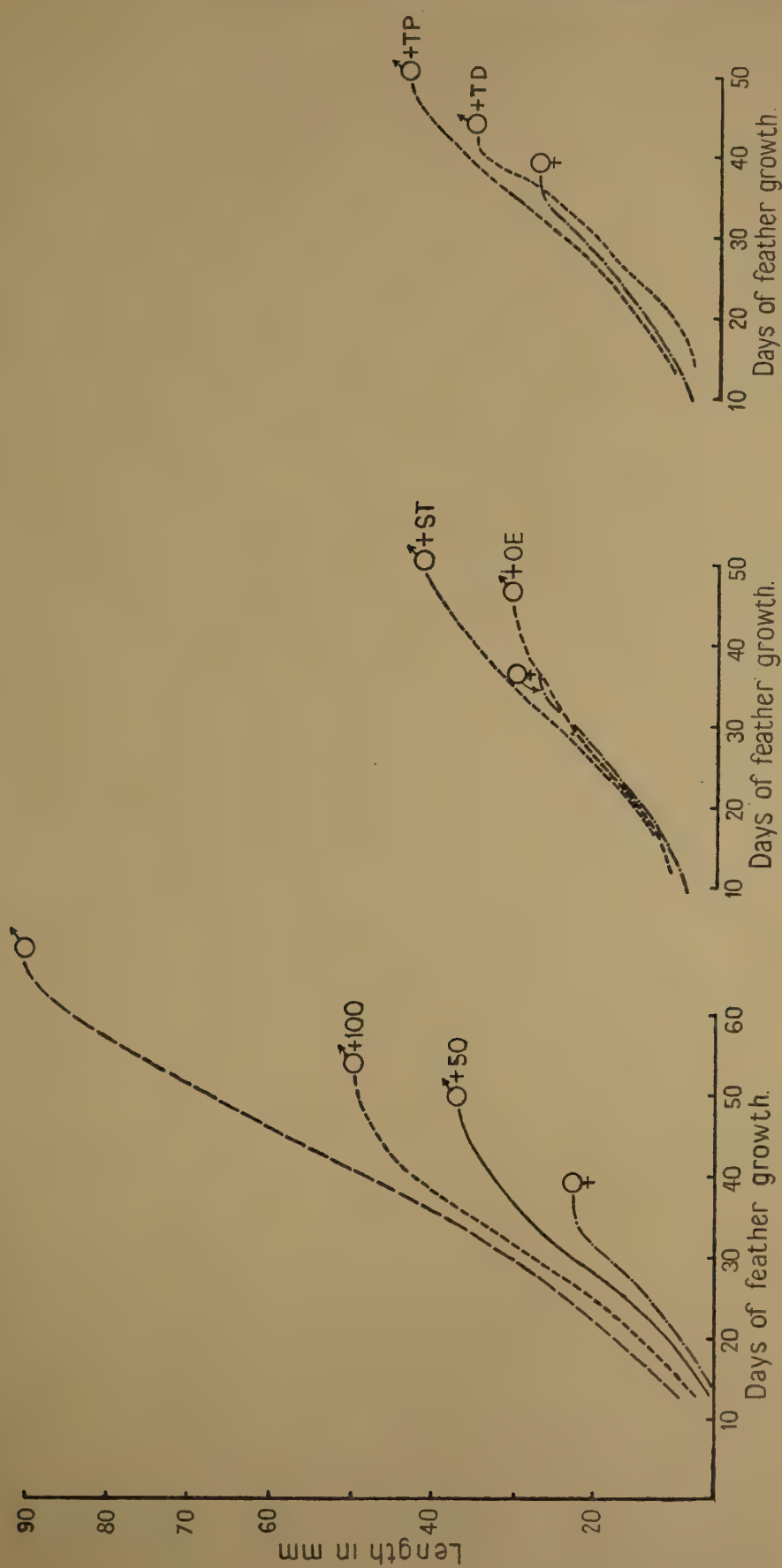
Growth rates and hormone thresholds of the normal and experimental feathers.

Growth rates in the pendent tract.

The growth curves of the developing feathers in this tract are shown in text-figs. 9, 10 and 11.

Text-figure 9 shows the growth curve of pendent feathers grown on the male with injections of 50 γ and 100 γ oestrone per day. The curves for the normal

Figs. 9-11.



9

Days of feather growth.

10

Growth curves of pendent tract feathers.

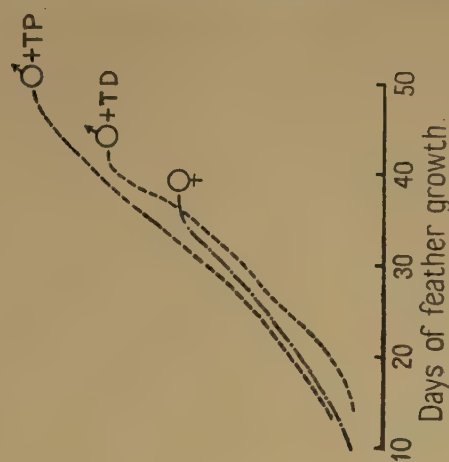
Normal male feathers.

Normal female feathers.

Male receiving 50 γ oestrone per day.Male receiving 100 γ oestrone per day.Male receiving 100 γ stilboestrol per day.Male receiving 270 γ stilboestrol per day.Male receiving 500 γ testosterone propionate every second day.Male receiving 7000 γ testosterone dipropionate per day.

11

Days of feather growth.



male and female feathers are given for comparison. For the sake of clarity the curves for feathers grown with the three smallest doses (2.5 γ , 5 γ and 10 γ oestrone per day) are not shown; they are very similar to the curve for the normal male, but in the feather grown with the 10 γ dose growth ceased earlier (at fifty-five days) giving a shorter feather.

The curves for the 50 γ and 100 γ oestrone doses show distinct modification in the direction of the female curve and are intermediate between the normal male and female curves. Once more the 50 γ dose (Experiment B 3) has given a greater modification than the 100 γ dose (Experiment C 98).

With stilboestrol (text-fig. 10) the growth curve is intermediate between the normal male and female curves, while with oestradiol (text-fig. 10) the curve is almost the same as in the normal female, except that growth continues for eight days longer giving a larger feather. In general text-figs. 9 and 10 show that the growth rates, growth periods and final sizes of male genotype pendent feathers decrease with increasing doses of oestrogenic hormones.

The growth curves of male genotype feathers grown with the androgenic hormones are given in text-fig. 11. With testosterone propionate the growth curve, period of growth and final length are all intermediate between the normal male and female. With the testosterone dipropionate growth is slower than in the female at first but later becomes faster; the growth period and final size are both a little longer than in the female.

Growth rates in the back tract.

In the oestrone series the 10 γ dose produced a growth curve similar to that of the normal male but the growth period and final length of the feathers were similar to those of the female. With the 50 γ and 100 γ doses the growth rate increased so that the curves were at first close to that of the normal female; later, however, while the female curve flattens out gradually the two experimental curves continued to grow fast, and their growth periods were shorter (by seven days) than those of the female. In final length the 100 γ oestrone feather (text-fig. 12) is intermediate between the normal male and female.

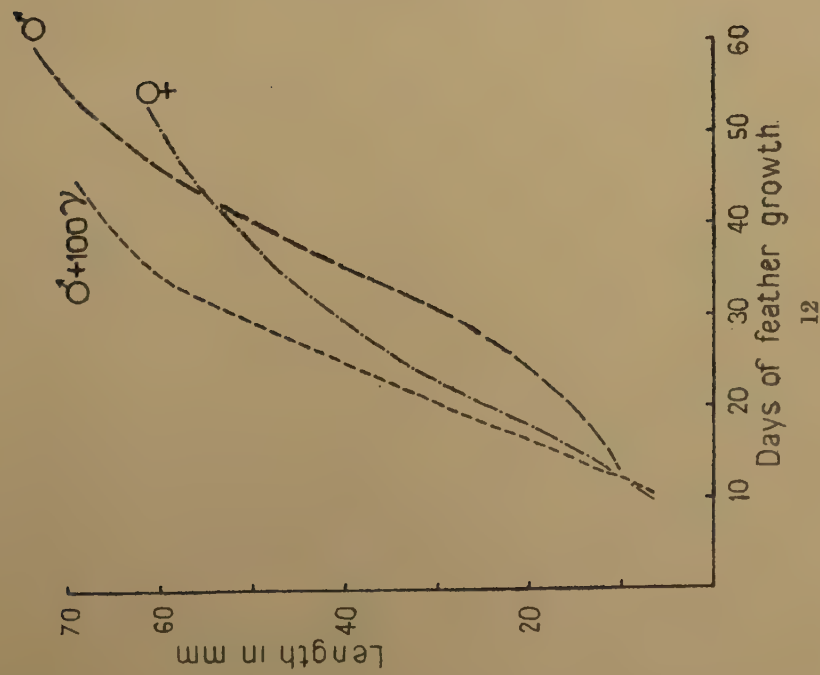
With stilboestrol and oestradiol growth of male back genotype feathers is faster (text-fig. 13) than in either male or female, and the curves are similar to those of male feathers grown with heavy injections of oestrone.

With testosterone propionate (text-fig. 14) growth is slower than in the female, and, for most of the period, than in the male. The final length is considerably shorter than in the female. With testosterone dipropionate, on the other hand, growth is faster than in the female and the growth period is shorter.

Growth rates in the saddle tract.

In this tract the differences between male and female growth curves are small. The male feather grows slower than the female at the beginning and faster towards the end of feather development. With a large dose of oestrone (100 γ per day) the curve takes on the female shape (text-fig. 15).

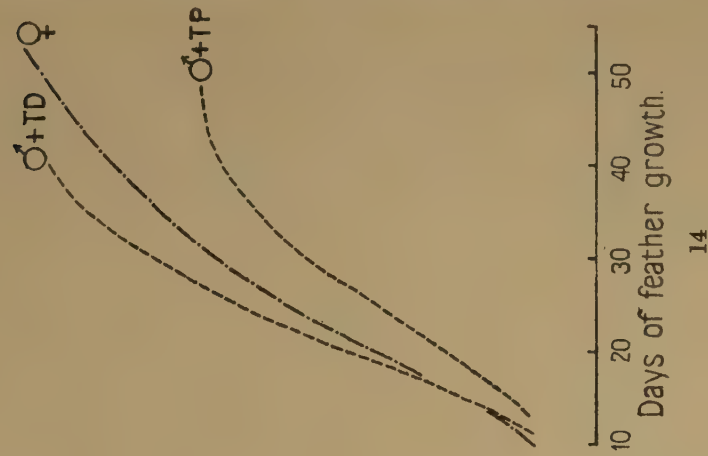
Figs. 12-14.



12



13



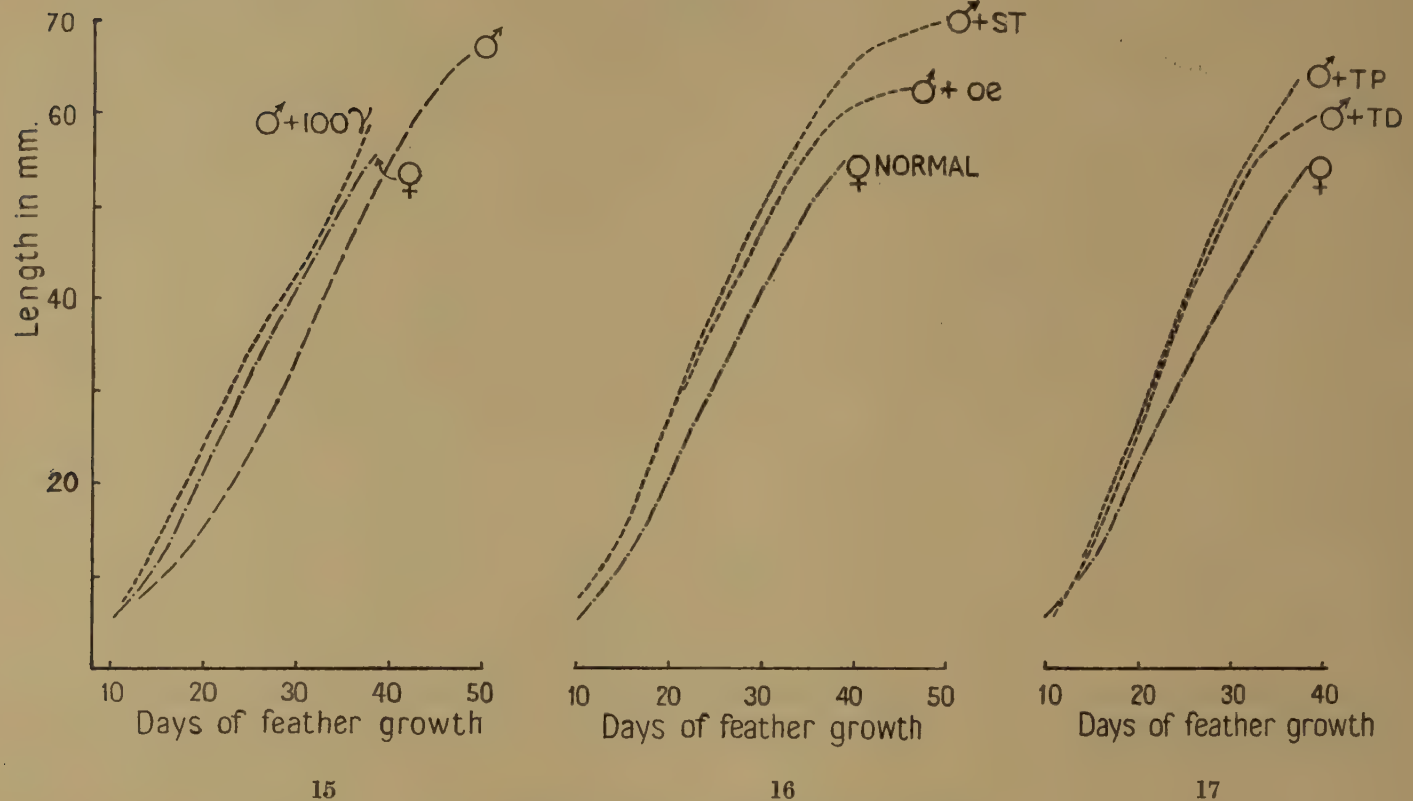
14

Growth curves of back tract feathers.
 Symbols as in text-figs. 9, 10 and 11.

With stilboestrol and oestradiol (text-fig. 16) the growth curve is similar in form to that of the female, but growth is somewhat faster, and the length of the feather and of the growth period are both greater.

The growth curves of male feathers regenerated in the presence of testosterone propionate and dipropionate are given in text-fig. 17. Apart from the small difference in final length these curves are similar. In both cases growth is faster than in the normal female.

Figs. 15-17.



Growth curves of saddle tract feathers.

Symbols as in text-figs. 9, 10 and 11.

In Brown Leghorn cocks Juhn, Faulkner & Gustavson (1931) found that the growth rates of the feathers varied from tract to tract, and they considered that these different rates were independent sex characters since they also appeared in capons. In Leghorn hens there was little or no regional differentiation in growth rates, and they concluded that the uniform growth rate of the female feathers was conditioned by the female hormone. Administration of oestrogenic hormone was followed by a decrease in the growth rate of anterior and posterior breast feathers in the capon, and by an increase in growth rate in the back and saddle. These induced growth rates thus tended to approach the more uniform rates of the normal female feathers. They also found that feathers in tracts with a high rate of normal growth required a larger dose to induce a female response

(a bar) than those with a lower growth rate, and postulated a direct relation between the growth rate of each tract in the male and its threshold of response to oestrogenic hormone. In their case the criterion of feminization was the production of a light melanin bar across the feather vane. In *Chrysolophus amherstiae* it is not possible to find an "all-or-nothing" response to the hormone in any character common to both sexes, as there are progressive steps in the response of the follicles of each tract.

Juhn, Faulkner & Gustavson (1931) and others have shown that in Leghorns, with oestrone injections, male soma feather follicles can produce wholly feminized feathers, but this does not occur in pheasants. Danforth (1937 b) found that in *Phasianus* feather follicles growing in the hormonal environment of the opposite sex have a pattern which has been described as intersexual (Crew & Munro, 1938). These feathers and those grown in the present experiments on male skin in an environment of oestrogenic hormone cannot be said to form part of a series leading to the normal female type. They are rather stages in an analogous series which is produced by male genotype follicles only. In *Chrysolophus* the growth curves of the normal female feathers varied considerably from tract to tract, and were not uniform as in Brown Leghorns. The feathers of the male tracts of *Chrysolophus* tended to have similar growth curves (although differing in growth period and final length) and the conclusions based on the study of Leghorn growth curves do not apply in the present case.

Comparison of text-figs. 9-17 shows that the action of the hormones on the growth curves of the feathers, whether direct or indirect, was not always one involving an increase in growth rate. In the saddle and back tracts the normal female feathers and, in general, those of the male grown with hormone injections, grew somewhat faster than those of the normal male. In the pendent tract, on the other hand, the female and the experimental feathers grew slower than the normal male feathers. Account must, however, be taken of the marked difference in final length of the male and female pendent feathers. This wide difference does not occur in Brown Leghorns where the differences between homologous male and female feathers are of approximately the same order as in the Amherst back and saddle tracts. In the male Amherst pendent feathers subjected to hormone dosage there was a marked reduction in the length of the feathers as well as a lowering in their rate of growth and period of growth.

It should be emphasized that the growth measurements only take account of increases in length and not of the growth of the shaft in diameter. In the developing male pendent feather the diameter of a 12-day pin feather was approximately 3 mm., whereas a female feather of the same age was only 1 mm. in diameter. In the presence of the larger doses of hormone the diameter of the male genotype pendent germ was much smaller than that of the normal male and approached that of the normal female. This determination of the initial size of the feather germ is therefore yet another character which may be modified in the presence of certain hormones. Greenwood & Blyth (1935) have shown that oestrogens and androgens act as direct endocrine factors and not through stimulation of the thyroid causing increased general metabolism. It is, in fact, difficult to see how in the

present case a general increase in the rate of metabolism could account for the different responses of the feather germ cells in each tract.

As a further step in the present analysis a series of measurements was made of the combined lengths of the three most distal cells of the subterminal iridescent median barbules of different pendent feathers (table 8).

TABLE 8.

Measurements (in μ) of the combined lengths of the three distal cells of subterminal iridescent median barbules. Pendent tract.

Genotype	Hormone environment	No. of measurements	Mean	Range
♂	Normal ♂	13	121	106-132
♂	10 γ oestrone daily	25	83	71-94
♂	50 γ oestrone daily	21	69	60-76
♂	270 γ oestradiol daily	20	80	69-86
♀	Normal ♀	18	65	58-70

These measurements show that homologous barbule cells in the female and in the experimental feathers of the pendent tract were significantly shorter than those of the normal male, and that the reduction in length of these cells in the experimental feathers was approximately proportionate to the dosage of hormones. It is suggested that one of the actions of the hormone may be to increase the rate at which the cells divide and differentiate. As the growth period is shorter in the experimental feathers such an increase in cell division rate would result in the production of smaller cells. A similar case has been reported by Montagna & Kenyon (1949) who found that testosterone propionate simulates mitotic activity in the sebaceous glands of the rabbit.

In *Chrysolophus* there is, therefore, no limen of hormone concentration above which the growth rate, barbule structure and final size of the pendent feathers become female-like in character. Instead there is an approximately graded response in these characters, depending on dosage, in all the experimental feathers. In pigmentation, the male pendent feathers (with a high rate of growth) require more hormone than the back and saddle feathers before light brown bars appear. In back and saddle feathers light brown pigmentation appears with daily doses of 2.5 γ or 5 γ oestrone, but in the pendent feathers this pigmentation is not induced until the dose is 50 γ oestrone per day.

There is no doubt, therefore, that for pigmentation change, the fast-growing feathers require a higher concentration of hormone than the slower growing feathers, that is, they have a higher threshold of reaction to hormones. This high threshold appears to be correlated not only with the rate of growth, but also, in the pendent tract, with the longer growth period and greater final size of the male feathers. It is probable that these three associated and measurable attributes play a part in determining the hormone threshold of the feather. The action of the hormone is considered to be one which inhibits the processes responsible for

these attributes, and there is evidence in favour of the view that this inhibitory action is one which increases the rate of cell division.

In the back and saddle tracts two of the attributes, final length and growth period, do not play such an important part, and the female-like bars are laid down in the male genotype feather when the growth rates are slightly greater than in the normal male. There is, therefore, a distinct difference between the growth-rate/pigmentation reactions of pendent feather follicles and those of back and saddle follicles.

Lillie & Juhn (1932) originally considered that the relation between growth rate and hormone threshold held for different parts of the individual feather germ as well as for the different areas of the body. They noticed that with small doses of hormone a reaction occurred only in that part of the vane which adjoins the shaft, while the barbs in the outer part of the vane remained male in character. They assumed that the low threshold of the barbs near the shaft (i.e. barb bases) was due to their low rate of growth, and that barb tips (more lateral on the vane) grew faster than the bases and therefore reacted only to higher concentrations. Lillie (1942) has now acknowledged that there is no evidence for such a differential rate of growth in barbs. Nevertheless the difference in reactivity across the vane is an observed fact and was also found in the present investigation, and there has hitherto been no other explanation of it. In the present investigation it has, however, been noticed that there is a difference in the size of the median barbules along the length of the barb. In general these barbules tend to increase in size with distance from the shaft (see table 9). This difference in barbule size is also reflected in the size of their constituent cells.

It has already been shown that barbule cells of oestrogen-treated male genotype feathers are smaller in absolute size than normal male barbule cells. It is possible that the same principle is at work in the present case and that the low hormone threshold of median barbule cells near the shaft is a function of their small size.

TABLE 9.

Male back tract. Iridescent dark green vane.

Length of the two distal cells (combined) of the median barbules.

	Distance of barbules from shaft in millimetres		
	1	5	10
Length of cells in μ . Means of 20 measurements	41	62	69

The growth curves also show that in normal male feathers of all tracts and in female pendent feathers there is a period of relatively slow growth at the beginning of feather development followed later by fast growth. In all these feathers there are iridescent structural features in the distal parts of the feathers. The iridescent structure has already been shown to decrease markedly as the proximal end of the vane is approached, even in the male back feather. The main iridescent features are in fact produced when growth is relatively slow. Iridescent features

and an initial slow growth period do not occur in female back and saddle feathers or in male genotype back feathers grown with large doses of oestrogenic hormones. It is only in the male genotype saddle feathers grown with oestrogens that iridescence occurs in the absence of a marked slow initial growth period. In these feathers, however, the area occupied by iridescent barbules is very limited and their production in development may constitute too small a factor to affect the observed growth curves. The initial slow growth period does not occur in the female back and saddle feathers which lack all trace of iridescence.

III. SUMMARY.

1. A brief account is given of the physical and chemical basis of colour in feathers, and of the process of feather development.

2. Analysis was made of the colour patterns and growth characteristics of normal male and female feathers in the pendent, back and saddle tracts of the Amherst Pheasant, *Chrysolophus amherstiae* (Leadbeater). Besides pigmentation particular attention was paid to the iridescent median barbules, which were described in terms of the lengths and widths of their reflecting surfaces. For comparison non-iridescent barbules were described in similar terms. Other characters which affected the feather patterns were final feather size, barring, growth rate, and growth period.

3. Feathers of the pendent, back and saddle tracts were grown on male Amherst Pheasants receiving different intramuscular injections of oestrogenic and androgenic substances (oestrone, oestradiol dipropionate, stilboestrol, testosterone propionate, and testosterone dipropionate).

4. In all three tracts feathers grown with injections of oestrogens or androgens were smaller than their normal counterparts. This disparity in size was most marked in the pendent tract. The experimental feathers thus tended to approach the size of the normal female feathers.

5. Pigmentation of all the experimental male genotype feathers was markedly different from that of the normal male feathers. In the pendent tract the originally white vane became pigmented with dark melanin in the presence of oestrogens and androgens. With increased dosage of oestrogen light brown bars were also deposited in the feathers of this tract. Where a light brown bar crossed an iridescent dark melanin-pigmented bar the colour of the latter was inhibited but its iridescent structure remained.

In the back tract regular light brown transverse bars were deposited in the presence of oestrogens, and there were traces of such bars in feathers grown with a large dose of testosterone dipropionate. In the saddle tract the yellow colour of the feather tip was lost in the presence of the hormones, and in the remainder of the vane light brown melanin was deposited as well as dark brown melanin.

6. Changes in barbule structure with hormone dosage were followed in greatest detail in the iridescent median barbules of the pendent subterminal bar. In general the hormones reduced the size of these barbules; with graded injections of oestrone the amount of reduction was approximately proportional to the dosage and to the

reduction in shaft length. Also in the pendent tract there is evidently some interaction between the injected hormones and the factors responsible for the deposition of the subterminal iridescent bar. For although the size of the iridescent median barbules of this bar was reduced in the presence of oestrogenic and androgenic hormones the torsion of these barbules and its associated iridescence was never completely lost. Furthermore the experimental pendent feathers and the normal male pendent feathers showed clearly that barbule torsion can exist in the presence of light brown pigmentation and even in the absence of all pigmentation. This observation runs contrary to Rensch's (1925 a) postulation of a causal connection between barbule torsion and heavy melanin pigmentation.

In the back tract the iridescent structure of the median barbules was completely lost in the presence of the oestrogens. In the saddle tract hormone-treated male feathers never lost the iridescent barbules of the subterminal bar, although there was some reduction in their size and number.

7. Barring patterns in the feathers studied were of two kinds: (a) those appearing in normal feathers of the male or of both sexes, and (b) those appearing only in female feathers and in male feathers grown with oestrogen injections.

In the pendent tract terminal and subterminal iridescent bars were well developed in the male and were present in reduced form in the female. In male feathers of this tract grown with oestrogens or androgens these bars were reduced in proportion to the reduction of the whole feather, but were never lost completely. The persistence of the torsion of the barbules of these bars has already been mentioned ((6) above).

In the saddle tract the subterminal iridescent bar of the male persisted in the presence of oestrogens. This bar did not occur in female genotype feathers.

In the back tract barring only occurred in normal female feathers and in male genotype feathers receiving injections of oestrogens. Differences in the angles shaft/bars were observed between the patterns of normal female and male genotype experimental feathers.

Analysis has shown that this difference is dependent upon the angle at which the barbs join the shaft, and it is considered that this angle is determined in the early feather germ, and that, in *Chrysolophus*, it is a sexual character unaffected by the hormonal environment.

8. The growth curves of the normal male feathers did not differ greatly from tract to tract except in the length of the growth period and the final size attained. The female feathers, on the other hand, showed greater differences in the rate of growth between the tracts. With injections of oestrogens and androgens the growth curves of the male feathers became similar to those of the normal female.

9. Some feathers showed a higher threshold of response to hormones than others. This high threshold was correlated not only with faster growth, but also with a longer growth period, greater final size, and larger cell size as measured in barbule cells. It is suggested that one of the ways in which oestrogens reduce the thresholds for these attributes is by increasing the rate of cell division and differentiation; since the growth period of the experimental feathers is shorter this would result in the production of smaller feathers.

Barbules and barbule cells near the shaft had a lower threshold of response to hormones than those more distant from it, and they were also smaller in size. It is suggested that the low threshold of response of the barbules near the shaft is correlated with the small size of the barbule cells.

In general, feathers with distal iridescent features had a low initial rate of growth, and it is possible that the morphogenesis of iridescence in feathers only occurs during periods of relatively slow growth.

10. A series of transplants between sexes was made with skin from the back and saddle regions of Amherst Pheasant chicks. Male skin grown on a female host yielded feathers similar in all characters to those of male feathers grown on a male bird receiving heavy doses of oestrogen. Female back skin grown on a male host produced dark almost black feathers, without the iridescence characteristic of a normal male feather, but with a little of the light brown melanin pigmentation of the type found in normal female back feathers. The pigmentation of these feathers (female skin on male host) suggests that the female feather germ may respond to the slight "feminizing" effect of the male hormones more readily than the male genotype feather germ, but the evidence is not conclusive.

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PLATE 1.

PLATE 1.

All feathers are from the Amherst Pheasant.

- | | | | |
|------|----|----------------|---|
| Fig. | 1. | Pendent tract. | Normal male feather. |
| | „ | 2. | Pendent tract. Feather grown on male receiving 2.5 γ oestrone per day. |
| | „ | 3. | Pendent tract. Feather grown on male receiving 10 γ oestrone per day. |
| | „ | 4. | Pendent tract. Feather grown on male receiving 50 γ oestrone per day. |
| | „ | 5. | Pendent tract. Feather grown on male receiving 100 γ oestrone per day. |
| | „ | 6. | Pendent tract. Normal female feather. |
| | „ | 7. | Back tract. Normal male feather. |
| | „ | 8. | Back tract. Feather grown on male receiving 2.5 γ oestrone per day. |
| | „ | 9. | Back tract. Feather grown on male receiving 10 γ oestrone per day. |
| | „ | 10. | Back tract. Feather grown on male receiving 50 γ oestrone per day. |
| | „ | 11. | Back tract. Feather grown on male receiving 100 γ oestrone per day. |
| | „ | 12. | Back tract. Normal female feather. |
| | „ | 13. | Saddle tract. Normal male feather. |
| | „ | 14. | Saddle tract. Feather grown on male receiving 2.5 γ oestrone per day. |
| | „ | 15. | Saddle tract. Feather grown on male receiving 10 γ oestrone per day. |
| | „ | 16. | Saddle tract. Feather grown on male receiving 100 γ oestrone per day. |
| | „ | 17. | Saddle tract. Normal female feather. |



PLATE 2.

PLATE 2.

All feathers are from the Amherst Pheasant.

- Fig. 18. Pendent tract. Feather grown on male bird after cessation of period of daily injections of 100 γ oestrone. Showing "after effect" of residual hormone.
- „ 19. Pendent tract. Feather grown on male receiving 100 γ oestrone per day during first half of growth period.
- „ 20. Pendent tract. Feather grown on male receiving 100 γ oestrone per day during second half of growth period.
- „ 21. Pendent tract. Feather grown on male receiving 270 γ oestradiol dipropionate per day.
- „ 22. Pendent tract. Feather grown on male which received three doses, each 200 γ oestrone in middle of growth period.
- „ 23. Pendent tract. Feather grown on male receiving 100 γ stilboestrol per day.
- „ 24. Back tract. Feather grown on male receiving 270 γ oestradiol dipropionate per day.
- „ 25. Pendent tract. Feather grown on male receiving 7000 γ testosterone dipropionate per day.
- „ 26. Back tract. Feather grown on male receiving 7000 γ testosterone dipropionate per day.
- „ 27. Saddle tract. Feather grown on male receiving 7000 γ testosterone dipropionate per day.
- „ 28. Back tract. Transplantation experiment. Female skin grown on normal male host.
- „ 29. Back tract. Transplantation experiment. Male skin grown on normal female host.
- „ 30. Back tract. Feather grown on male receiving 270 γ oestradiol dipropionate. Barbs to the right of shaft displaced artificially to take up a position perpendicular to the shaft.
- „ 31. Back tract. Normal female feather, with barbs to right displaced artificially to take up a position perpendicular to the shaft.
- „ 32. Back tract. Feather grown on male receiving 100 γ stilboestrol. Barbs to the right of shaft displaced artificially to take up a position perpendicular to the shaft.
- „ 33. Saddle tract. Transplantation experiment. Male skin grown on normal female host.



**The growth-stages of the pouch-young of the Native Cat (*Dasyurus viverrinus*)*
together with observations on the anatomy of the new-born young.**

By

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(With Plates 1-13 and 3 figures in the text.)

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* Now *Dasyurus quoll* Zimmermann, 1780 (*vide* Tate, 1947).

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PART I.

THE GROWTH-STAGES OF THE POUCH-YOUNG.

INTRODUCTION.

Although our knowledge of the external characters of the pouch-young of various species of marsupials is now fairly extensive, thanks to the work of the authors included in our reference list, of no single species do we possess a detailed illustrated account of a continuous series of growth-stages of the pouch-young ranging from the new-born to the adolescent individual.

The present paper attempts to fill this gap in our knowledge, so far as concerns *Dasyurus*

The material at our disposal was collected by one of us (J. P. H.), with the aid of grants from the Government Grant Committee of the Royal Society, during the years 1895-1905, when he was Demonstrator of Biology in the University of Sydney. It comprises an ample supply of pouch-young, ranging from the new-born, still unattached young to the adolescent individual, four months old.

This material we have grouped into seventeen stages, labelled A-P. The description of these stages forms Part I of this paper, and whilst we are jointly responsible for it, the senior of the two authors wishes it to be stated that jointly does not signify equally, since by far the major part of the detailed descriptive work involved was undertaken by W. C. O. H., utilizing the grouping into stages and the descriptive notes and records concerning them, drawn up by J. P. H. in Sydney.

The beautifully executed pencil drawings of the pouch-young reproduced on Plates 1 & 2, were made by Mr. A. Cronin of Sydney.

For Part 2, observations on the anatomy of the new-born young, J. P. H. is responsible. He desires to thank Professor J. Z. Young, F.R.S., for the facilities generously afforded him in the Department of Anatomy and Embryology, University College.

The Native Cat, during the period mentioned above, was still common in New South Wales and could be caught fairly easily in baited traps. The adult females sent in by collectors, if they had young in the pouch were either killed and the young, together with the reproductive organs, pouch and mammary glands preserved or kept alive until the young reached a desired stage. Females without young, after the condition of the pouch had been noted, were placed each in a cage with a male and kept under close observation, the pouch being examined and a note made of its condition at fairly regular intervals. They lived well in captivity and many of them bred, yielding the material on which were based the papers of

Hill (1900, foetal membranes, placentation, mode of parturition, new-born young), Sandes (1903, corpus luteum), Hill (1910, early development), O'Donoghue (1911, growth-changes in the pouch and mammary glands, prior to and during lactation), O'Donoghue (1912, corpus luteum), Hill & O'Donoghue (1913, reproductive cycle) and also the pouch-young dealt with in the present paper.

Here we may deal briefly with certain matters pertinent to the present communication.

THE POUCH AND THE MIGRATION THERETO OF THE NEW-BORN YOUNG.

The pouch normally contains six teats, arranged in two lateral rows of three, but the number is subject to slight variation. Hill & O'Donoghue record that in over 120 females examined, one pouch contained five, two had seven and five had eight teats, the remainder had six. Osman Hill (1951) also records a specimen with eight teats. Six is accordingly the normal number of young that can be accommodated in the pouch but for one reason or another, there may be less than six. On the other hand, there is evidence that more young may be born than can find place in the pouch. We may recall two such records, already mentioned in the Hill and O'Donoghue paper. Female killed 28.VIII.98, had six young attached to the teats, three more were lying free inside the pouch, and one, somewhat shrivelled, lay just outside the pouch, a total of ten young. The second record is much more striking. Female 20.10.VII.02, killed sixteen days after coition, brought forth a total of eighteen young. Of these, six were found attached to the teats, one lay free in the pouch alongside an attached one and eleven were found clinging to the hairs round and directly below the opening of the pouch.

Apart from producing, for *Dasyurus*, a record number of young, this female is of interest in another connection, to wit, the method by which the new-born young reach the pouch. Here was clear evidence pointing to the conclusion that the new-born young find their *own* way unaided to the pouch and are not transported there by the mother with the aid of her lips as was at that time currently believed. But, owing apparently to the inhibitory action of that belief, the significance of the evidence was not appreciated at the time and it remained for Dr. Carl Hartman and his wife to witness, in 1920, the birth of a young opossum and to observe it crawling by its own efforts over the hair of the mother, all the way from the cloacal opening to the pouch, a distance of "full three inches". Hartman's paper (1920) constitutes the first authentic record in a scientific periodical of how the young marsupial reaches the pouch, but still earlier, in 1913, A. Goerling in a letter to the *Western Mail*, Perth, W.A. (reproduced in full in Dr. Hartman's paper) described how he had observed on 25th February 1906, the new-born young of the Red Kangaroo (*M. rufus*) making its own unaided way to the pouch, "using its arms in its progress and continually moving its head from side to side, thus assisting the upward movement". He states it took the young one nearly thirty minutes to reach the top of the pouch, "the last end in a semi-circle." McCrady (1938) in his *Monograph on the embryology of the Opossum* confirmed Hartman's observations and supplemented his account of the crawling movements (p. 183). These, he states, begin with the flexion of the head and neck (say to the left), followed by the forward movement of the right fore-limb.

The head begins to move to the right, the claws of the digits of the right manus are flexed and catch hold of the hairs and the right fore-limb makes its back-stroke, propelling the young one forward and at the same time the caudal end of the body is flexed to the right. The left fore-limb is now thrown forward, the head being flexed to the right and the cycle is repeated. Thus by the alternate over-arm movements of the fore-limbs, accompanied by contra-lateral movements of the head, the young one is propelled forwards head first, and at the same time upwards (probably guided by the sense of smell, *vide* p. 417) until eventually it reaches the pouch.

Subsequent observers (*vide* Hartman, 1952) have provided confirmatory evidence so that the long discussed problem of how the new-born marsupial reaches the pouch is now finally settled.

But before leaving it, and as a matter of historical interest, we would call attention to two sentences in Dr. Barton's paper of 1806, already quoted by Dr. Hartman (1952). He writes (p. 350 of reprint):—"The young opossums, unformed and sightless as they are at this period [immediately after their exclusion from the uterus] *find* their way to the teats by the power of an invariable, a *determinate* instinct",* and he adds in a footnote "it is not true, as has often been asserted, that the mother with her paws puts the young ones in the pouch". *Contra* Dr. Hartman (*loc. cit.*, p. 93), we can only interpret these two sentences taken together as evidence that Dr. Barton had actually seen the new-born young of the opossum in process of crawling to the pouch by their own efforts and to him would seem to belong the credit of having been the first to have done so and the first to place his observations on record†.

THE NURSING PERIOD.

Hill & O'Donoghue (1913, pp. 152-153) distinguished two phases in the nursing or lactation period in the marsupial, i.e. the period during which the young nourished by the milk secreted by the mammary glands of the mother. These are:—

(1) the period of fixation, during which the lips are fused and the nipple, the free end of which becomes bulbously enlarged, is enclosed in the buccal cavity so that the young one cannot become detached. This period in *Dasyurus* extends over about seven to eight weeks;

(2) the free period. Round about stage M, when the young are just over two months old or even earlier, when the young are about seven weeks old, their lips become free and they can leave the nipple at will but are still wholly dependent on the mother's milk. At stage O, when the young are about three months old, their eyes are open (they would seem to open in young mid-way between stages N and O) and they are able to crawl about outside the pouch but are still dependent

* This sentence is also quoted by Owen (1841, p. 325) without comment but with the insertion of "(qu.?)" after "instinct". Owen probably meant the query to apply to the whole sentence and not to "instinct" alone, since he believed the mother transported the young one to the pouch by her lips.

† It has to be remembered that Dr. Barton conveyed this information in a *letter* to his correspondent and presumably intended to include a full account of his observations in a proposed memoir which he does not appear to have completed.

on the mother. At fifteen weeks, the young are now quite active outside the pouch and begin to feed on meat, though no doubt they continue to suckle. At four months (stage P), the young are adolescent both as regards their external characters and their disposition since they now snap vigorously on the slightest provocation.

The nursing period in *Dasyurus* thus extends over about fifteen weeks.

If we compare the foregoing data with those provided by Dr. Barton (1806), Hartman (1928), Langworthy (1928), and McCrady (1938) for the nursing period in the Opossum, we find there is a fairly general agreement between the two, but in *Dasyurus* it is somewhat longer than in the Opossum, as might be expected in view of the fact that the new-born young of the former is developmentally much less advanced than that of the latter.

In the Opossum, the period of fixation lasts some fifty days (McCrady, *loc. cit.*, p. 198). The young one is at the end of that period "about the size of a mouse and has a short and sparse coat of fur".

The free period begins with the freeing of the lips when the young are between fifty and sixty days old. At this time also ("about 50 or fifty-two days", Barton), the eyes open (earlier than in *Dasyurus*) and the young begin to crawl about on the mother's body, (also earlier than in *Dasyurus*), but they cannot yet control their body temperature and do not leave their mother (McCrady, *loc. cit.*, p. 201).

At sixty-seven days, the young now the size of young rats and fully haired, can run about actively and climb with agility (Langworthy). They continue to suckle until they are about eighty days old. Shortly after this, when the young are eighty to ninety days old, they are weaned but remain with the mother for some time longer. Hartman and McCrady agree that it probably takes at least ninety days to raise a litter to a state of independence.

In the Opossum, the nursing period would appear to extend over about twelve to thirteen weeks as compared with about fifteen weeks in *Dasyurus*.

THE SUPPOSED MAMMARY COMPRESSOR ACTION OF THE CREMASTER MUSCLES.

The view that the milk is forced into the buccal cavity of the pouch-young marsupial by the contraction of the cremaster, or as Duvernoy termed them in 1811, the ilio-marsupialis muscles, has been so widely accepted and has become so firmly imbedded in the text-books, ever since it was put forward by Seiler and Morgan in 1828, that it has come to be regarded as an established fact. But in recent years, owing largely to the increase in our knowledge of the capabilities of the new-born marsupial, and especially of its sucking capacity, doubt has been cast on its validity by several observers (Enders, 1935; McCrady, 1938; Hartman, 1952).

The historical setting of this belief is of some little interest.

The idea that the milk is injected into the buccal cavity of the attached pouch-young seems to have been first put forward by Geoffroy Saint-Hilaire in 1826. He examined the isolated pouch of a Kangaroo, with a young one attached to the nipple, and was surprised to find that the external layer of the latter was provided with a sheath of muscle. He concluded that the milk filling the nipple was injected into the buccal cavity of the pouch-young by the contraction of this muscular sheath and the muscles situated in the skin of the pouch. Then, in 1828, a paper

by Seiler appeared in Oken's *Isis* and in the same year, Morgan communicated a paper to the Linnean Society (published in 1831), in which the authors included observations on the anatomy of the cremaster muscles in the female Kangaroo, the former terming them the ilio-marsupialis muscles or preferably the "Hüftbein-Brustdrüsen Muskeln" and the latter the "compressing muscles". Both arrived, independently, at the conclusion that these muscles when they contracted, compressed the mammary glands over which they spread and so forced the milk through the nipple into the buccal cavity of the attached pouch-young. Morgan considered such a mechanism was rendered necessary by the imperfect state of organization of the latter, whilst Seiler thought that the usual method of sucking could not operate, owing to the nipple projecting so far back into the buccal cavity.

The conclusion these authors reached was, of course, based on their study of the relations of the muscles in question to the mammary glands but their attempt to find an explanation of these relations was based on premises which are not wholly acceptable to-day, for, although the new-born marsupial is, on the whole, a poorly organized creature, it is not so helpless as most of the older workers supposed it to be and we have long known that it is capable of suction, for how otherwise could the tip of the nipple get inside its buccal cavity.

The conclusion of Seiler and Morgan as to the function of the cremaster muscles was accepted by Owen (1840, p. 212) who referred to them as the mammary constrictors. Other writers have termed them the compressor mammae. Katz (1882) in his valuable paper on the abdominal wall and the organs related to it in marsupials summarized previous work on these muscles and described their anatomical relations in *D. viverrinus* (pp. 652-654 & Taf. 38, fig. 12), largely confirming the observations of Seiler and Morgan. Taking origin from the ventral edges of the ilia in front of their articulations with the sacrum, the muscles emerge through the inguinal canals, pass under the anterior portions of the marsupial bones and spreading out fan-wise over the mammary glands, blend with each other across the middle line as Morgan had observed in the Kangaroo. In regard to their function, Katz reached the same conclusion as Morgan and Seiler and believed that in contracting, they exerted strong pressure on the mammary glands and so caused a flow of milk for the sustenance of the young, at least during the early period of their pouch-existence.

So far as we know, that view remained unquestioned until 1935 when Enders in a paper on mammalian life-histories quite incidentally made the statement (p. 409) that the pumping action "variously ascribed to the cremaster 'ilio-marsupialis' or panniculus carnosus" is "more than problematical", without offering any evidence in support of it, stating only that "the matter will be taken up in a paper on the ventral musculature of the Didelphid Marsupials", but neither in his paper of 1937 on this subject nor in that of Langworthy (1932) is specific mention made of the cremaster muscles.

McCrady (1938) in his monograph on the development of the Opossum again raised the question, stating (p. 188) that "in the opossum, there seems to be no mechanism for the pumping of milk" and this in spite of the fact that Duvernoy, according to Katz (*loc. cit.*) described and figured the cremaster muscles in the

Opossum so long ago as 1811 and that Katz himself had provided confirmatory evidence, stating that they are similar in their relations to those of *Dasyurus* (*vide* also Carlsson, 1903). McCrady is of the opinion that "the pumping of milk is not universal and is only a supplemental mechanism if it occurs", the new-born young one being capable of sucking.

Hartman (1952, pp. 115-116) states that Enders investigated the problem of "milk-pumping" by the methods of dissection and electrical stimulation and failed to obtain positive results. The evidence, he considers, is unquestionably against the "pumping" theory, but the experimental evidence not being available to us, we can form no opinion of its validity. We do not know, for example, whether Enders stimulated the genito-crural nerves in a lactating female, which, according to Cunningham (1882), innervate the cremaster muscles, and with what results.

There the problem must rest for the present so far as concerns the pouched marsupials but before leaving it, we would call attention to the conditions obtaining in the pouchless didelphids which appear to militate against the old theory or at all events, its applicability to the marsupials as a whole.

In *Monodelphis henseli*, for example, the nipples vary in number from seventeen to twenty-five (Thomas, 1888; Bresslau, 1912) and are arranged in a caudo-median group of five and two lateral rows, comprising each from six to a maximum of eleven nipples, the formula in the type specimen being 11-5-9=25 (Thomas, 1888). The lateral rows begin shortly in front of the cloacal opening and extend forwards into the thoracic region (Thomas, *loc. cit.*, Pl. XXVIII, fig. 6). Here, then, there can be no question of a general compressor action on the part of the cremaster muscles, located as these are in the pelvic region.

Carlsson (1903) appears to be the only investigator who has examined these muscles in pouchless species. She states (p. 502): "Bei *Didelphys pusilla* [= *Marmosa pusilla*, with 11-15 nipples] und *D. sorex* [= *Monodelphis sorex*, with 13 nipples] . . . ist der Muskel rudimentär. Er kann weder auf die vordern Zitzen, ihrer Lage wegen, noch auf die hintern, in Folge seiner Verkümmernng, als ein compressor mammae wirken, sondern der Hautmuskel scheint seine Funktion übernommen zu haben". The latter assumption, we should hesitate to accept without further evidence nor do we think the words "rudimentar" and "Verkümmernng" should be used in connection with the weakly developed cremaster muscles in these forms, suggestive as they are of a secondarily derived condition.

It may, of course, be argued that, when the pouch was eventually evolved, the cremaster muscles acquired a new importance in relation to the now concentrated mammary glands, but however that may be, we can but agree with McCrady that the old view of the compressor action of these muscles does not hold generally for the marsupials. It is certainly inapplicable to the pouchless didelphids but whether it must be discarded also for the pouched marsupials, future investigation must decide.

Since the above was written, we have been able to make a dissection of the cremaster muscles in a lactating female specimen of *Dasyurus* kindly presented to one of us (W. C. O. H.) by Dr. A. G. Lyne of Tasmania.

The muscles are very well developed forming a fan-shaped sheet as described by Katz (*loc. cit.*). From their lateral attachment in the flank, each muscle proceeds ventrally, superficial to the epipubic bone and, at the lateral margin of the weighty mammary gland, splits into two laminae, superficial and deep, enclosing the gland. The superficial lamina splits further into three distinct parts, a broad anterior moiety, a narrower intermediate and a slender posterior one. None of these could be traced to the median line. They insert aponeurotically just medial to the lateral limit of the gland. The deep lamina sweeps over the dorsal aspect of the gland and ends in fascia, but its anterior fibres seem to be connected with a cutaneous invagination at the cranial pole of the gland.

From the above arrangement of fibres, mechanically it seems possible for the muscles to act as compressors of the mammae, but the more obvious function appears to be as a sling to the hypertrophied glandular tissue—possibly preventing its ventral displacement or herniation. No muscular connection with the nipples could be demonstrated macroscopically. Further work is in progress on the problem.

AGEING OF STAGES.

The ages attributed to the various stages are to be regarded as only approximate. Parturition in *Dasyurus* usually occurs during the night so that the attached young observed early on the following morning are already a variable number of hours old—possibly as much as twelve hours. The unattached young, found inside or outside the pouch, provide the actual stage of the new-born young and have afforded a basis of comparison with recently attached young from twelve or less hours old to twenty-four hours old. The ages of later stages were arrived at by keeping alive females with recently attached young in the pouch and measuring the young at noted intervals. In this way, dated growth-records were obtained and from there, the approximate ages of the stages were calculated.

SYSTEMATIC DESCRIPTION OF STAGES A TO P.

Stage A. The new-born young. (Pl. 1, fig. 2.)

The material for this stage is derived from four females : (a) 28.VIII.98, with six young attached to the nipples, three lying free in the pouch (stage A)+one, shrivelled lying just outside the pouch ; (b) 20.10.VII.02, with eighteen young, six attached, one free in pouch, +eleven clinging to the hairs round and directly below the opening of the pouch ; (c) 1.VII.05, with three attached young ; (d) 9.27.VII.02, with three attached young +one unborn.

Measured fresh in the curved attitude attached to teat, they average about 7 mm. long from anterior extremity of head to rounded posterior end of body. In the living state they are of a faint pinkish or reddish tint, semitransparent, except where vessels shine through the integument. In the living young, the pulsation of the heart is distinctly visible as well as the respiratory movements. The head length is about 2.75 mm. After spirit fixation the greatest length from snout to rounded hinder end is 5.5 mm.—6 mm. and the head-length 2.5 mm. Each fore-limb reaches 1.5 mm. long, but the hind-limb only 0.75 mm., and the tail about 1.0 mm. The weight (average of four) is 12.5 mg.

The great discrepancy in development between the anterior part of the body and the fore-limbs on the one hand and the whole hinder region is very marked and characteristic.

The head is bent at right angles to the trunk and is characterized by the large oval nares, directly laterally, with the long axis passing from above downwards and backwards. The lips are fused laterally, the line of junction being very distinct but the fusion does not quite extend to their anterior limits. Medially they are far apart, leaving a large triangular opening guarded by a thick transverse lower lip and two halves of the upper lip separated by a median cleft. As in the Opossum, as noted by Selenka (*loc. cit.*), there is an oral shield (Schnabelschild) surrounding the buccal opening and shaped in such a fashion as would enable it to act as a washer or suction pad, serving thereby to anchor the embryo to the skin of the pouch surrounding the base of the nipple. Structural details of this are discussed below (p. 380) together with a criticism of Selenka's and McCrady's views on its significance. The eyes at this stage, represented by the secondary optic vesicles and lens, are scarcely visible, being covered by epidermis. No choroidal pigment is present in sections. The rounded lens can be seen in fixed material. The external auditory meatus is marked by a depression bounded posteriorly by an upper, larger and a lower, smaller tubercle. In the unattached young the tongue projects slightly.

There is no neck protuberance, but between the fore-limbs is a bladder-like "cervical" swelling with thin semi-transparent walls, arising from the thorax and extending anteriorly to the floor of the mouth, and having a diameter of 1.5 mm. in its longest axis. Its histological structure is considered hereafter (p. 382).

The fore-limb is robustly built, held out stiffly from the body in a ventral direction and with the palmar aspect of the manus directed posteriorly. No elbow joint is indicated. Digits are well indicated, rather short and blunt and all but the small hallux provided with slender, recurved, very sharp, deciduous claws which are nearly 0.5 mm. long.

The hind-limb is more flipper-like, with a short basal segment and a distal pedal plate with the plantar surface pointing medially. Digits are not yet indicated.

Along the median line of the belly the line of fusion of its two developmental halves is clearly visible and the position of the umbilicus distinctly recognizable.

Compared with the new-born *Didelphis* (Selenka, 1887; Hartman, 1928; McCrady, 1938; Osman Hill, 1951) the present species is much smaller, the new-born Opossum averaging about 11 mm. in G.L. (McCrady, p. 198) but agrees in the square cut muzzle, presence of the oral shield and advanced pectoral and retarded pelvic development, although the digits of the hind-limb are indicated in *Didelphis*. The median cervical swelling does not occur in the latter and seems to be peculiar to *Dasyurus*.

The new-born young of *Perameles nasuta* is altogether much more robustly built and much larger than that of *Dasyurus*, measuring in G.L. 14 mm., whilst the recently born young of *Macropus major* is larger still; according to Owen (1834, p. 344), "the whole length from the nose to the end of the tail, when stretched

out, did not exceed 1 inch 2 lines". As depicted (nat. size) in his fig. 5, Pl. VII, the crown-rump length of the young one is about 23 mm. See also Dollman (1938).

In the *Perameles* young, the digits of the hind-foot are all indicated, the fourth being the largest. In the *Macropus* young, Owen describes the short hind-limb as having "the three divisions of the toes now distinct". Examination of the uterine embryos of several species of Macropods, shortly before birth, shows that these three divisions comprise (a) the small syndactylous second and third toes, (b) the very large fourth toe, and (c) the smaller fifth toe, all better defined than the corresponding digits in the *Perameles* young.

Stage B. Estimated to be about 7 to 12 hours old. (Pl. 1, figs. 3 and 4.)

The description of this stage is based primarily on the pouch-young of female 28.VI.97, with six young attached to the nipples and measuring in G.L. about 7 mm. The living young were slightly reddish in colour and the heart pulsations were distinctly visible. Attachment to the nipple is not yet very firm, for one young one dropped off the nipple before, and another after immersion of the pouch in the fixative.

In pouch-embryos of 7 to 7.5 mm. greatest length (measured fresh) there is little advance on the new-born condition. The general appearance much resembles the neonatus, but there is an overall increase in size and certain changes in detail. Measured after spirit fixation the following data are obtained:—

Greatest length varies from 5.75 to 6 mm.	
Head-length	3.00 mm.
Fore-limb	1.75 mm. long.
Hind-limb	1.00 mm. long.
Tail	1.50 mm. long.

The weight of two specimens together was only 20 mg. giving an average of 10 mg., i.e. slightly less than stage A.

In one specimen of this series, possibly the one referred to above which first dropped off, the mouth retained the triangular shape of stage A, and the tongue was just visible, resting on the lower lip. In all the rest the mouth has changed to a circular opening through its firm application to the nipple while no trace of tongue is to be seen. The lower jaw now projects slightly beyond the upper and the head is more raised off the thorax, so that it appears of greater length. The snout is becoming more prominent and the line of fusion of the lateral parts of the lips less distinct. The site of the eye is just recognizable with the lens. The external auditory meatus is less marked than in stage A, being now a shallow depression bounded behind by a pinna of no more advanced development than in A, but the inferior tubercle is rather less apparent.

The fore-limbs are widely divaricated, as in stage A, and directed palms backwards, and slightly dorsally. Pedal digits are still not indicated. The trunk is generally shorter and more arched dorsally. This is to be explained doubtless by the enlargement of the thorax through the initiation of pulmonary respiration and to the imbibition of the serous-like secretion of the mammary

gland into the alimentary canal—features to which McCrady (1938) drew attention in *Didelphis* as distinguishing late prenatal from early postnatal stages.

Stage C. About 30 hours. (Pl. 1, fig. 5.)

The description of this stage is based on the attached young of ♀ 28.VIII.98, which furnished the unattached young stage A, the attached young being killed after an interval of twenty-four hours, and on those of ♀ VI.04 with six young.

This stage is attained about thirty hours after birth. The crown-rump length measured about 3.5 mm. In spirit preserved specimens the greatest length is reduced to 6 mm. and head-length to 3.25 mm., but there is a slight individual variation. The fore-limb is now 2 mm. long, but the hind-limb about the same as in the previous stage.

The whole animal is more robust in appearance, weighing on the average about 22 mg. The head is more ovoid in form, convex above and below, and the trunk stouter than in earlier stages. A distinct sucking mouth is present, prolonged slightly forwards, spout-like, below the teat, which is firmly fixed within the buccal cavity. The snout is more prominent and the nares relatively smaller. The highest part of the head is now at the occiput rather than anteriorly, and there is a distinct depression between the convexity of the neurocranium and the projecting muzzle. Position of eye (covered with epitrichium) and ear is just recognizable with difficulty. The external auditory meatus is shallower and less distinct.

The deciduous claws are still present in the specimen drawn (fig. 5) but at this stage or soon afterwards they begin to be shed. Their structure and functional significance is discussed at length below (p. 382).

In one specimen of *Dasyurus* (VI.04) out of a clutch of six, the left third and right fourth digits retained a claw, but the rest had lost all theirs.

The hind limb in stage C is still paddle-like, but its margins are slightly and very faintly crenated—the earliest external indication of digit-formation.

The cervical swelling between the fore-limbs is now much reduced.

At a slightly later period—probably about thirty-six hours after birth (stage C')—the embryo weighs 22.5 mg. (average of two) and the crown-rump length in spirit preserved material attains 6.5 mm. and head-length 3.1 mm. The general appearance is as for stage C, with an even greater tendency to robustness of body. The cervical swelling is considerably reduced and its surface wrinkled. Claws were still present on all the four lateral digits of the manus in the two available specimens, showing that there is some temporal variation in respect to their shedding. The tail is now short conical and curved, with a bluntly rounded tip. No evidence of a genital tubercle is present. The hind-limbs are no more advanced than in C. In another batch of about the same development, but possibly a few hours older, all the manual claws have been shed, leaving the digits with sharp uncornified tips. Crown-rump length of the batch is 7 to 7.5 mm., head-length 3.5 mm. and weight 31.5 mg. In another batch of the same stage (between C and D) average weight of two is 30 mg. These are probably under forty-eight hours old.

Stage D. 3 days. ♀ 24.VIII.98 with four young. (Pl. 1, fig. 6.)

During the third post-natal day this stage is attained. There is little increase in the crown-rump length, 7 mm. being the average, the largest specimens not exceeding 7.5 mm. The head-length, however, has increased up to 4 mm. and the weight is now 50 mg. The fore-limb is 2.5 mm. long and hind-limb 1.75 mm.

The body is strongly curved and robust in appearance, the snout being more prominent than in stage C and more distinct from the neurocranium. Reduction in the external nares continues, these openings being now more circular in outline. The eye is more distinct, but nevertheless visible only with difficulty; it presents a very faint pigmentation through the epithrichium. In sections, pigment granules are now present in the pigment layer of retina. The position of the auditory opening is not now distinguishable. The cervical vesicle has all but disappeared.

The abdomen measures 3.5 mm. in transverse diameter as compared with about 2 mm. in stage C.

The fore-limbs now terminate in short, stumpy conical digits which are blunt-ended and without claws. The manus is demarcated by a marginal depression especially marked on the ulnar side, from the proximal part of the limb; but no elbow is indicated as yet externally. The hind-limb shows the pes demarcated similarly, but the pedal expansion is a flattened plate, though digits are now indicated as marginal round-topped elevations separated by indentations of equal depth. The tail lies in the same position as before, flexed forwards between the roots of the hind-limbs; it is much longer and narrower, being 2 mm. in length.

Stage E. 5 to 6 days. ♀ 9.VII.97, with the exceptional number of seven young. (Pl. 1, fig. 7.)

The following data apply to pouch-young of five to six days old. The weight has increased to 70 mg. (average of four) but some litters include individuals of 66 mg., which may be even older and slightly more advanced developmentally than those chosen as typical for this period. The overall length averages 8 mm. with individuals up to 8.5 mm. and the head length 4.5 mm. (in spirit-preserved material).

The snout is distinctly more prominent than heretofore, and the general form still more robust than in stage D, the head especially being stouter, thicker and longer. The dorsal contour forms an uninterrupted convexity from the crown to the rump, where it increases in degree gradually and progressively towards the tail.

The nostril is further reduced, and the eyelids are beginning to separate, a palpebral slit being formed through which the eyeball now appears distinctly pigmented. The position of the external auditory meatus and pinna are just recognizable. The mouth remains circular and its lips are firmly adherent to the nipple.

The fore-limbs are not much increased in length, but appreciably in girth, and an elbow is just recognizable near the attachment to the trunk. The forearm

retains its earlier position, with the palms directed posteriorly. The digits are now short and broad, conical with fairly acute tips without claws.

Pedal digits are now more marked, III and IV being larger than the others. The plantar surface is still directed mesially. The hind-limb projects straight and stiffly from the trunk and shows no evidence of segmentation, being perfectly cylindrical except for slight medio-lateral flattening of the pes. Between the roots of the two hind-limbs is a prominent transversely ovoid swelling—the genital tubercle.

Stage F. About 7 days old. ♀ 29.VII.98, with seven young. ♀ 1.28.VII.02 with five young, killed seven days after birth. (Pl. 1, fig. 8.)

Living specimens of about a week's post-natal growth measure on the average 9.5 mm. long and have a head-length of 5.5 mm. Individuals may attain 10.5 mm. extreme length. Measured after spirit preservation the greatest length varies from 8.5 to 9 mm. and the head-length 5 to 5.5 mm. The weight varies from 70 mg. (average of two in one litter) to 88 mg. (average of three from another litter), or even up to 0.11–0.12 gm. in slightly more advanced litters (stage F').

Morphologically there is not much advance shown on stage E except for the generally greater bulk. The head is tending to lose its barrel-like shape. The fore-limb now measures 2.5 mm. long and the hind-limb 1.5 mm. The former terminates in four well-defined, short, conical digits ending bluntly. This is not yet a definitive claw. Sections show that the epidermis is provided with a thin cornified layer, and a curious thickening on palmar side shortly behind the tip of the digit. These claws differ from the temporary claws in not being recurved. Digits III and IV are typically the largest, but II may be as long as IV and III shorter than either. A vestigial pollex is represented on the radial border by a slight tubercle. No evidence of palmar sculpturing is to be seen, the whole palm forming a uniform convex plane. The hind-limb differs little from that in stage E, except for its increased robustness.

Stage G. About 10 days old. ♀ 12.VII.99, with four young. (Pl. 1, fig. 9.)

At this age pouch-young, of characteristic clumpy form, measure, when fresh 11.5–12 mm. total length (crown–rump) the majority being in the shorter category. The head-length attains 6.0 to 6.7 mm. Each weighs 0.185 gm. (average of four). In some litters at the same developmental stage specimens of head-length up to 7 mm. have been noted.

Apart from the continued increase in bulk and robustness of head and trunk, the only advance on stage F is in the hind-limb. This is increased considerably in length (2 mm.) especially in the pedal segment, though digits II–V are much as in F, but rather more distinct. The plantar surface is still directed medially, but there is a slight marginal indentation at the site of the ankle-joint.

The manus is much as in F, but there is now a tendency for the palm to turn mesially, though the main direction is still posteriorly. The tail is stouter, but retains the same position—continuing the dorsal convexity. There is no change in the genital tubercle.

Stage H. About 14 days old. ♀ 23.VII.97 with six young. ♀ 6.VIII.02, young killed fourteen days after birth. ♀ VI.04. (Pl. 2, fig. 10.)

The degree of curvature of the spine—though still forming an arc of a circle—varies somewhat individually at this stage, and onwards, so that the crown-rump length shows a fairly considerable range of variation. As pointed out in a previous communication (Osman Hill, 1951), the head-length provides a more reliable indication of stage of development. On the average the maximum length is around 13.5 mm. and the head-length 8.0 to 8.5 mm. The weight in one litter was 0.18 gm. (average of two) and in another 0.29 gm. (average of three).

The head is larger in proportion to the trunk and is now becoming raised above the fore-limbs, due to the lengthening of the neck. The snout is more distinct than in stage G, due to the increasing prominence and separation by a dorsal notch from the dome-like cranium; the epidermis of the snout is, moreover, of a different texture from that on the rest of the head, having a smoother appearance and a slight pigmentary deposit. The mouth is now relatively extremely small, the lip-groove being just distinguishable under the lens as a longitudinal slit-like depression in the epitrichium. Nares are relatively large, more rounded than oval, but posteriorly the margin is very depressed, and the depression is continued dorsally as a groove.

Very faint indications of papillae, visible only in very oblique illumination, are to be detected on lips and cheek. These are the first indications of the development of vibrissae.

The ear is marked by a tubercle, bounded anteriorly by a groove—apparently the pinna shining through the epitrichium. From the tip of the muzzle to the anterior border of the pinna the distance is 4.5 mm.

The fore-limb is considerably more elongated than in previous stages, measuring from hinder border of attachment to tip of longest digit 5.25 mm. There is a suspicion of an elbow and also of an ulnar "carpal" hillock—the latter just proximal to the marginal wrist depression. Four digits are clearly indicated, III and IV the largest, as well as a very small pollex. All five are provided with short, blunt claws. The whole limb is now pressed backwards stiffly so that the palms look towards the abdomen. The dorsum manus almost makes contact with the cloacal or genital tubercle, which is thus wedged between hands and tail.

The hind-limb has grown considerably in length, due particularly to an increase in the pedal segment, which is now more clearly demarcated from the thick, short, subconical basal segment. Its length is almost 3.5 mm. of which the foot makes up 2.25 mm. The limb projects stiffly ventralwards, but there is some attempt at flexion at the ankle, though the plantar surface is still medially directed. A calcaneal prominence is present, and the four digits are now clearly defined, III and IV the largest. There is but the slightest indication of claws.

The genital tubercle is now very distinct, projecting forwards from the anterior cloacal margin beyond the anterior margin of the hind-limb. It ends in a broad tip.

The tail continues the curve of the back and attains 2.5 mm. long.

Stage I. 19 days old. (Pl. 2, fig. 11.)

This stage corresponds to the earliest stage represented in the Royal Scottish Museum collection discussed previously by one of us (Osman Hill, 1951). It was there assumed erroneously that this represented the recently born condition.

The crown-rump length now varies from 14 to 16.5 mm., most specimens being around 15 to 15.5 mm. Larger specimens of 17 mm. from vertex to mid-lumbar region (summit of flexure) are intermediate between stages I and J.

Head-length of typical stage I is 10 mm. in the living. The weight is 0.5 gm. (average of two) at stage I but increases up to 0.867 gm. (average of two) in intermediate examples between stages I and J.

Morphologically there are many advances on stage H, notably in the shape of the head and elongation of the neck. Head and trunk are now nearly proportionate as regards size. The elongation of the head specially affects the region behind the snout, the latter being much as in stage H, but more distinctly pigmented in some embryos than others. External nares are more advanced, approaching the adult condition. The position of the eye is hardly more expressed than in the previous stage. The pinna is more clearly defined, forming a small triangular flap with its apex directed forwards, and though still covered with epitrichium, it stands out much more than heretofore. The epitrichium had disappeared from the lower part of the pinna in one single embryo. In front the pinna is bounded by a shallow depression deepest ventrally.

Papillae connected with the development of tactile vibrissae are distinct on the mystacial group and also indicated for the genal and submental groups. The two last mentioned take the form of raised epidermal pads with only the feeblest trace of individual papillae. The mystacials, however, consist of discrete papillae arranged in six more or less horizontal rows. The two uppermost rows are very oblique and their anterior papillae pass dorsally to the posterior margin of the naris and so fall into the category of what Wood Jones (1951) has in the foetal tarsier referred to as rhinal papillae. The first row has three papillae only, the second six. Then follows a more horizontally disposed row of six papillae of which the most anterior lies opposite the lower part of the posterior narial margin. Three more rows of seven or eight papillae each lie parallel to one another and to the margin of the upper lip.

In the fore-limb (5.5 mm.) the wrist is now plainly indicated, and the digits are now completely separated from each other and provided with strong, almost hoof-like blunt claws. On the palmar aspect of the manus, the five tactile elevations are discernible, two proximally, rather feebly marked, and three distal or interdigital pads, all subconical and circumscribed. There is also, proximal to the wrist crease, a large ulnar carpal elevation. The tips of the digits beneath the claws are now ball-like from formation of apical tactile pads. These specializations are thus far lacking from the sole, apart from the swelling of the apices of the digits. Digits are also nearly fully separated in the hind-limb and are nearly of equal size, III and IV very slightly predominating; these two now have blunt claws. The limb is 4.5 mm. long from anterior border of attachment to tip of longest digit.

The sex is now distinguishable externally, for in the male the scrotum is recognizably separate from the penis, lying a little anterior to the latter, forming a small bilobed mass surrounded by a circular groove. In the female the marsupium is indicated as a shallow depression bounded by a circular groove. Its floor appears raised into six elevations, three on each side, of irregular shape and size.

The tail is now about 5.5 mm. long. The dorsal curved length of the body from snout to root of tail is 38 mm.

Stage J. 25 days old. (Pl. 2, fig. 12.)

This is an exceedingly characteristic stage as regards attitude of the embryo in the fresh condition. The dorsal length, from snout to root of tail is 4.75 cm. The crown-rump length is 20 mm. but varies according to the amount of curvature. Head-length averages 12.5 mm. Body weight averages 1.0 gm. each (average of two).

The head now looks disproportionally large, the thickness, from frontal region to floor of mouth being 9 mm., compared with only 6.5 mm. in stage I. In general appearance the head is now approaching a cat-like condition, with prominent snout separated behind by a distinct notch from the frontal region—more marked than in previous stages. The external nares are large and sigmoid in shape. There is a very distinct median sulcus between the nostrils traceable inferiorly to the entrance of the funnel-like mouth, but there is as yet no specialization of the rhinarium.

Vibrissae are erupting from the papillae of the mystacial group, being more advanced in the rhinal and upper labial rows, and not yet visible in the two lowest labial rows. A few stray hairs of the vibrissae type also appear on the cheek just behind the middle rows of the mystacial set. Short fine contour hairs have also erupted on top of the head. The genal and interramal groups do not seem to be any more advanced than in stage I. These developments compare favourably with Wood Jones' (1920, 1922) reports on *Trichosurus* and *Pseudochirops*, where the vibrissae appear at about the 50 mm. stage, but this author points out that papillae are well marked prior to the appearance thereon of the vibrissae—at 35 mm. in *Pseudochirops* and 32 mm. in *Trichosurus*, where the ulnar papilla is first to appear.

The labial sulcus extends backwards to a level below the anterior margin of the eye. Eyelids are still fused, a shallow groove indicating the line of fusion. The triangular ear pinna is a thickish fold with its apex pointing rostrally, and bounded by a broad, shallow sulcus. The tip, however, is now quite free and can be passively raised.

The fore-limb measures 8 mm. long from the inferior border of its attachment to tip of longest digit. Its axis is directed caudally and the palmar surface towards the belly wall. The five digits are somewhat flexed around the periphery of the palm. They are short, plump, sausage-shaped and terminate in strong claws. The latter are now more fully erupted, having lost their hoof-like character, showing a strong dorsal axial convexity, the tips thus pointing ventrally. They

are also strongly convex in the transverse dimension. Apart from greater prominence the palmar pads show no advance on stage I. The carpal hillock is well indicated, but no vibrissae are erupted upon it.

The hind-limb is 7 mm. long, and from knee joint to tip of longest toe is 4 mm. The four digits are quite separate and their terminal claws are in the hoof-like stage, being less advanced in eruption than on the manus. The feet approach the muzzle on account of the rather acute flexion of the lumbar region. The plantar surface shows three slight elevations corresponding to the interdigital touch pads, but there is little indication of proximal pads. The heel is better marked than in earlier stages and the knee also more clearly defined.

The tail measures 7 mm. long. In the male the penis is 2 mm. long and the scrotum is a small elevation rising only 1 mm. above the surface. It is no longer bilobed, but is surrounded by a groove of oval outline.

In the female the marsupium is an oval shallow depression, wider anteriorly and ending bluntly behind. It is surrounded by a ridge of thickened epidermis. The floor has three rounded elevations on each side. The clitoris is essentially like the penis, but smaller.

Between stage J and stage K (i.e. about 35 days old) a number of litters are available (=stage J' (Pl. 2, fig. 13)); these correspond very closely in development to the second of the three stages described in the former contribution dealing with the Edinburgh collection. The dorsal curved length of these measures 5.2 cm. and the maximum antero-posterior length of the much curved body 23 mm., head-length, 13.5 mm. The weight at this period varies from 1.4 to 1.92 gm.

Chief advances are in the differentiation of the rhinarium and in the further freeing of the external ear, the details of the latter having been fully described in the paper quoted. In some specimens it is quite free and commencing to rotate backwards. Vibrissae are no further advanced, but the general pilous covering has advanced from the frontal region downwards to the lips and mental region, but no body hairs are yet erupted. Tactile pads are now fully differentiated on the planta.

Stage K. About 41 days old. (Pl. 2, fig. 14.)

The following measurements are recorded to show the advance in size :—

Crown-rump length	around 29 mm.
Maximum dorsal curved length from snout to root of tail	60-63 mm.
Head-length	18 mm.
Snout to tip of pinna	16 mm.
Snout to anterior palpebral canthus	6 mm.
Thickness of head	11.5 mm.
Length of pectoral limb	13.0 mm.
Length of pelvic limb	11.5 mm.
Length of pes (to ankle)	6.5 mm.
Length of tail	12 mm.
Weight varies from 2.68 to 3.6 gm.	

The mouth is now a distinct oval with the long axis transversely. It is guarded by thick, hairless skin continuous above with the now fully differentiated rhinarium. The lips are beginning to separate laterally, the labial groove being deep and very distinct—even when separation is not evident. Posteriorly, the groove ends below the eye. A short groove extends from the supero-lateral edge of the mouth upwards and laterally, delimiting the rhinarium below; the skin covering the face below this groove is hairy, except where it borders the mouth opening. The rhinarium is sharply demarcated on the dorsum nasi by a deep transverse groove, behind which the hairy part of the dorsum nasi is raised, almost forming a hood. There is thus no evidence of the naked backward extension of the rhinarium described in the adult *Dasyurus maculatus* (*vide* Osman Hill, 1948). The differentiated rhinarium already shows, however, some indication of the characteristic rhinoglyphic pattern, chiefly in the form of shallow transverse internarial sulci without clear papillary elevations on the intervening fields, though there is a faint trace of papillation on the dorsum. The rhinarium is otherwise smooth and marked in the median line anteriorly by a shallow vertical sulcus which gradually broadens towards the mouth.

Elsewhere on the head pale golden hairs are visible to the naked eye, at least as far back as the fronto-parietal junction. In some specimens the haired zone ends in a fairly straight line just in front of the ear, curving thence forwards to the posterior end of the labial furrow. Below this the mental region alone has these larger hairs. The ear itself is naked, and so is the subauricular and immediately post-auricular skin. On the dorsal aspect of the head, behind the fronto-parietal junction, extending also down the nape, and trunk as far as the root of the tail, fine hairs are present that can be seen only on magnification. These are very short, whitish or colourless and leave large naked tracts between them. More occur on the interramal region behind the mental zone and on the extensor aspect of the fore-limb. On the lower back the eruption is less advanced than anteriorly, but a few are just visible on the dorsum pedis. Vibrissae are no more advanced than in stage J, except for increase in length of those already erupted.

Completion of the eruption of hair in *Dasyurus* seems to occur in relatively smaller pouch-young than in the genera described by Wood Jones (1920, 1922 a, b). In *Trichosurus* the hair is first visible at 32 mm. vertex-rump length, but at 80 mm. a new secondary growth has taken place and the primary hairs have also elongated. Pigmentation is fully developed at 100 mm. In *Isodon* the hairy covering is complete at 92 mm., and in *Pseudochirops* at 92 mm.

Practically all the hairs so far erupted show the primitive craniocaudad trend in direction. The floor of the mouth is the only exceptional region. Here, there is a distinct broad, median tract with the cranio-caudad slope, bordered each side by a tract converging towards the median tract from the lower lip and cheek. On the hindmost part of the lower lip, just beneath the angle of the gape, is a small bunch of hairs erupted perpendicular to the surface and therefore without any directional slope. Some longish hairs similar to these occur on the interramal tubercle, but cannot be classed as vibrissae. A similar adornment occurs on the ulnar carpal tubercle.

Eyelashes are very distinct on both lids, although the latter are still marginally fused.

In older examples the hair eruption is somewhat more advanced and it is even possible to detect by naked eye some appearance of the coat pattern, in the form of white spots among the darker patches. In these examples certain additional vibrissae have also appeared.

The external auditory meatus is still occluded by an epithelial plug, but the pinna is directed backwards and beginning to show its epithelial sculpturing. Its tip is more rounded than pointed. Near its base anteriorly is a small rounded tubercle and slightly in front of this a low vertical fold of epidermis. This marks the anterior limit of the meatus.

As regards general bodily form, in stage K, the foetus is rapidly approaching that typical of the grown animal, with the head more elongated, though as yet bluntly truncated in front. The trunk is losing its acutely flexed posture, so noticeable in stage J, though there is still a fair amount of curvature at the mid-abdominal level.

Both pairs of limbs are making rapid progress, particularly the hinder. The manual digits all show pointed recurved claws, those on the pes being now strong and slightly recurved. An extensive lunule is visible on all the claws. On the concave ventral side of each claw is a softer triangular hyponychium. All the palmar and plantar pads of the adult hand and foot are now defined, but the palms and soles are quite unpigmented or otherwise adorned.

In the male the scrotum is now freely pendulous forming a pear-shaped sac 1.5 mm. in diameter with short pedicle. The penis measures about 2.5 mm. long and shows a differentiation into glans and body, the glans being thinner than the body.

In the female the marsupium measures longitudinally 2.5 mm. and transversely at its cranial end about 2 mm. Narrowing posteriorly, it is not demarcated by groove or otherwise from the general integument. Its floor presents a shallow median groove, whilst laterally another groove separates the floor from the lateral bounding ridge. This groove according to Bresslau (1912) is formed by the cranio-caudal fusion of the "marsupial pockets" of earlier stages.

The clitoris is now 2 mm. long and differentiated into a terminal blunt conical glans which is quite smooth, and a basal swollen portion whose surface is wrinkled. The cloacal opening is a very narrow cleft immediately posterior to the clitoris.

Stage L. About 46 days old. (Pl. 2, fig. 15.)

The foetus has now attained the following dimensions :—

Crown-rump length	42.0 mm.
Maximum dorsal curved length (snout to root of tail)	71.0 mm.
Head-length	21.0 mm.
Snout to tip of pinna	20.0 mm.
Snout to anterior palpebral canthus	7.3 mm.

Thickness of head	13.5 mm.
Length of fore-limb	15.0 mm.
Length of hind-limb (flexed)	15.0 mm.
Length of pes	7.5 mm.
Length of tail	17.5 mm.
Length of penis	2.5 mm.
Length of clitoris	2.0 mm.
Body-weight (average of three)	4.28 gm.

This stage corresponds therefore to the largest in the Royal Scottish Museum series previously described.

The mouth is still very narrow, but the lateral lip-line is deep, though the lips there still fused. Eye and ear are but little different from those in stage K, but the head as a whole is smaller in proportion to the trunk, the neck more defined and elongated and the muzzle more demarcated from the posterior part of the head. The ears, however, show some pigment, and there is commencing excavation of the external auditory meatus.

Chief advances are in the pilous system. Head and dorsal aspect of trunk are now distinctly hairy and the back very clearly shows the spotted pattern. The ground colour is tawny brown, the spots being white, the hair here being rather shorter than on the brown tracts. Hair is present over the major portion of the rest of the body, but less obvious, as it is shorter and colourless. Areas over the hinder portion of the interramal region, the hindmost portion of the trunk and a patch just over the elbow joint appear hairless to the naked eye, but the lens reveals very short hairs on all three. The tail, however, is truly hairless and so are the pedal digits and a small portion of the neighbouring dorsum pedis, as well as the pinna. The lateral aspect of the thigh may also appear hairless.

As regards the direction of hairs, there is indeed little disturbance from the primitive cranio-caudad trend anywhere. On the dorsum nasi the hairs are porrect, and the same applies to those on the mental region, and behind this, also to the interramal vibrissae rising through the neighbouring short hairs. A curious single line of almost vertically implanted hairs forms an isolated tract anterior to the base of the pinna. It is separated from the general hairy covering of the preauricular region by a vertical naked field. Dorsally the hairs become more oblique pointing dorsad and then somewhat backwards, the tract arching over the pinna to join the main cranio-caudad stream of the vertex. On the lower cheek the hair streams slightly ventrally as well as backwards, skirting thus the lower part of the ear. Eyelashes stand out distinctly by virtue of their direction and by their deeper pigmentation. There is an isolated tuft of three or four short vertical hairs on the tragal hillock, otherwise the pinna is destitute of hair.

Vibrissae are present but not well marked. The mystacials are recognized merely by their greater length. They are scarcely more robust than contour hairs. The same applies to the interramals. The genal group, situated on a tubercle below and behind the eye are more distinct in some individuals. A tubercle just above the wrist bears a few longish tactile hairs directed post-axially.

Claws on the digits of manus and pes are now all sharp and recurved.

Both penis and clitoris now show distinct differentiation into body and glans. The scrotum has a transverse diameter of barely 2 mm.

The marsupium is an ovoid depressed area measuring 2.5 by 2.5 mm. It is bounded on each side and cranially by a prominent raised pouch-fold. The centre of its floor is slightly elevated and on each side are three localized swellings indicating the nipples, or at least the mammary primordia of Bresslau.

Stage between L and M. About 60 days old. ♀ 20.VIII.00, young killed fifty-nine to sixty days after birth.

In specimens representing a phase between stages L and M of which material from five distinct litters is available, there are some important advances on stage L quite apart from size increments. The body weight in one of these litters averages 5.23 gm. and in another 6.93 gm. In the last there is distinct progress in the rhinarium and in the commencing freeing of the lips. The mouth is now sufficiently enlarged to permit protrusion of the tongue, whose broad squarish crenated apex is thrust forwards rather like a newborn puppy's.* Beneath the tongue is a median thickening terminating just short of the apex in a number of papillae. The apex linguae presents a broad, shallow, median notch, and the neighbouring margin is provided with enlarged globular papillae.

The definite rhinoglyphic pattern now adorns the rhinarium, corresponding exactly with that described for the adult (Osman Hill, 1948) except for the absence of the posterior extension of the dorsum nasi so well shown in many adult marsupials (e.g. *Perameles*, *Thylacinus*, Boardman, 1943, 1945). The rhinarium is sharply demarcated from the upper lip by a sulcus which produces a deep notch below, where it meets the labial margin. The median notch is also very marked, but the median groove proceeding dorsad therefrom just fails to meet the posterior boundary of the rhinarium dorsally.

Vibrissae are much more clearly differentiated from the contour hairs than in stage L. Eyelids are still fused. The pinna is larger, less lobate, due to its greater extent and corresponding proportionate thinness. Its surface sculpturing is better marked. Anterior to it are two overlapping vertical cutaneous folds bearing short hairs on their summits. The upper is the longer, and the lower short and more lobate, with its upper extremity slightly posterior to the lower end of the long fold. The short fold seems to be homologous with the tragus, as it borders the notch which leads to the meatus. Naked tracts separate these folds from normally haired neighbouring skin. Elsewhere the pinna is hairless as in stage L.

* (1) ♀ 20.VIII.00, when killed had two young only in the pouch (G.L. 4.8 cm., H.L. 2.3 cm.), but when examined two days previously three young were present, one on the nipple, the other two free—but though the lips were still fused, the young opened their mouths sufficiently and grasped hold of the nipples, with the aid of their tongues.

Stage M. Aged a little over 2 months. (Pl. 2, fig. 16.)

The dimensions of examples taken from litters at this stage are as follows :—

Crown-rump length	55.0–60 mm.
Maximum dorsal curved length (snout to root of tail)	86.0 mm.
Head-length	28.0 mm.
Snout to tip of pinna	27.0 mm.
Snout to anterior canthus	9.4 mm.
Thickness of head	16.8 mm.
Length of free fore-limb	20.0 mm.
Length of hind-limb	27.0 mm.
Length of pes	13.0 mm.
Length of tail	25.0 mm.
Length of penis (free part)	2.0 mm.
Length of clitoris (free part).....	1.5 mm.
Body-weight	10.2 gm.

The foetus is now completely hairy in all parts where hair occurs in the adult ; and the spotted pattern is fully established.

The lips are now completely free laterally to the angulus oris, but eyelids are still fused, though the upper has differentiated further than in stage L and is now folded. The pinna is now haired, the hairs pointing backwards and upwards on the upper half and backwards and downwards on the lower half. The vertical folds anterior to the pinna are more fully developed than in the stage intermediate between L and M. The meatus is still occluded.

The penis is now relatively shorter but thicker, due to sinking back within the prepuce. The glans is more fully differentiated and appears like a tubercle on the posterior part of the organ. The scrotum, rather more than 2 mm. in diameter, is now slightly bilobed.

The clitoris is similar to the penis but somewhat smaller. The marsupium resembles the last stage described, but is more triangular in outline, with the apex directed caudally. The boundary folds are now much more robust, but smooth and convex. Nipples are still low tubercles. The marsupium is bounded by a raised naked cutaneous fold describing a triangular outline. The base lies cranially and is formed by a thicker fold than the two lateral elements. The latter meet caudally in an angular commissure, between the lips of which is a slight somewhat deeper fold resembling a fleshy fourchette.

Stage N. Barely 2½ months old. ♀ 30.X.96, with four young. (Pl. 2, fig. 17.)

Measurements at this period average as follow :—

Crown-rump length	53–65 mm. (according to extension)
Maximum dorsal curved length (snout to root of tail)	100.0 mm.
Head-length	33.0 mm.
Snout to tip of pinna	31.5 mm.
Snout to anterior canthus	11.5 mm.
Thickness of head	18.0 mm.

Length of free fore-limb	30·0 mm.
Length of free hind-limb	38·0 mm.
Length of pes	18·0 mm.
Length of tail	30·0 mm.
Length of penis (free part)	1·5 mm.
Length of clitoris (free part).....	1·2 mm.
Body-weight	12·5 gm.

The pouch-young is now a small replica of the adult, the head being more elongate and pointed. All the facial vibrissae are now well shown and also the carpal group. Eyelids are still united at their margins, but manifestly just ready to separate.

The pinna is more folded and the rounded tubercle located just above its centre is now free except at its base. This seems to correspond to the supratragus (metatragus) of other mammals. It is, however, overshadowed dorsally by a hood-like, well-raised, narrow, transverse fold which seems to arise by an exaggeration of the upper part of the antihelix, and thus would appear to be homologous with the lower crus antihelicis of man. This interpretation is supported by the presence above the fold of a slight depression (scaphoid fossa) beyond which is a less well-defined eminence corresponding to the human crus antihelicis superior. The helix is formed from the upper anterior vertical fold and the tragus from the shorter lower fold of earlier stages. Behind the latter, the notch leading to the auditory meatus is much depressed. The whole pinna is now quite hairy, most of the hairs being colourless.

The penis and clitoris are now quite short elevations in proportion to the general body proportions, the former being slightly the larger. The marsupium is about 4 mm. in diameter and forms a raised discoidal area with a central depression. Its margins and floor are now hairy. Bounding folds are less defined than in stage M.

Stage O. About 3 months old. ♀ 24.IX.95, with four young.

At three months after birth, the pouch-young is capable of creeping about freely outside the pouch, and at fifteen weeks is quite active and feeding on meat. It measures from vertex to root of tail 95 mm., and in head-length 45 mm. Fore-limb 38 mm. long; hind-limb 41 mm. (in flexed position), pes 27 mm. and tail 56 mm. The thickness of the head has grown to 23 mm.

The body, and especially the head and back, are thickly hair-clad, and in addition to the ordinary vibrissae, there is a crop on the mental region and immediately below the mouth.

Eyes are now open and the pinna fully differentiated in all its parts, with a deep external auditory meatus. The tip of the ear is once again turned forwards.

The penis is now relatively small, appearing as a thick blunt projection about 2 mm. long immediately in front of the cloacal opening. The clitoris is similar in appearance and position, forming, however, merely a rounded tubercle. The scrotum is quite conspicuous, in contrast to the penis, being 4·5 mm. in diameter.

The marsupium is more depressed than in stage N, 6·5 by 5·5 mm. in diameter, and fully hairy, the nipples being obscured by the hair. O'Donoghue (1911) has given an account of the structure of the pouch at this stage. He states (p. 194) that it has the form of a shallow circular depression on each side of which are situated three nipple primordia. In section, these appear as hollow invaginations of the epidermis (the nipple pockets of Bresslau), formed by the hollowing out of the mammary primordia. From the bottom of each pocket there arise six hair-follicles, from the medial side of the upper or proximal portion of each of which arises a downgrowth, the mammary gland primordium, and a little later, below the latter, a second outgrowth arises from the follicle-wall, the sebaceous gland primordium. Still later, the nipple pocket is evaginated to form the definitive nipple.

Stage P. 4 months old. Single specimen labelled 6.XI.99, adolescent in its characters and disposition. Now snapping savagely.

Measurements of this single male are as follows :—

Maximum length (snout to root of tail)	165·5 mm.
Crown-rump length	135·5 mm.
Maximum dorsal curved length to root of tail	225·0 mm.
Head-length	60·0 mm.
Snout to tip of pinna	69·0 mm.
Snout to anterior canthus	30·0 mm.
Thickness of head	27·2 mm.
Length of free fore-limb	58·8 mm.
Length of free hind-limb	78·0 mm.
Length of pes	42·0 mm.
Length of tail	102·5 mm.
Length of scrotum	10·8 mm.
Body-weight	175·0 gm.

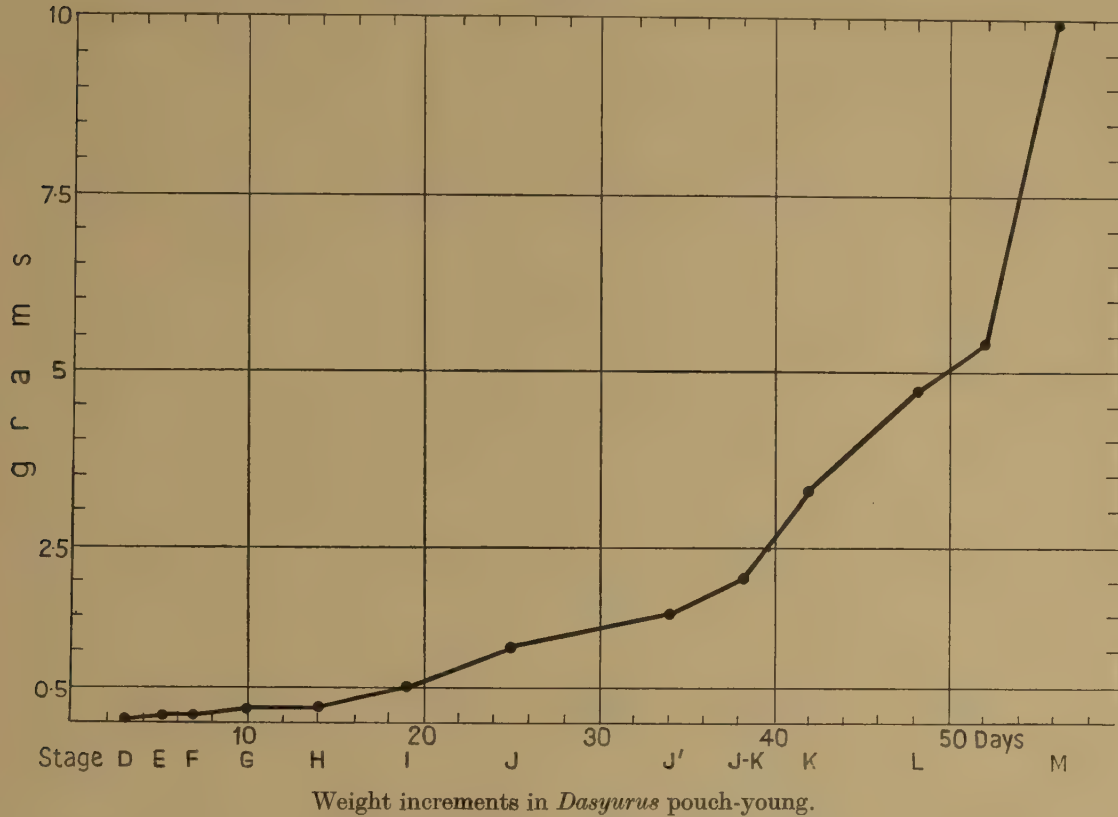
(a) *Growth of the pouch-young.*

Three graphs are presented herewith demonstrating the progressive increase in size of *Dasyurus* pouch-young from first entry into the pouch until the age at which they are ready to vacate it. In the first two charts the weight increments are plotted against age; in the third the head-length is plotted against age. We discarded graphs based on snout-rump length as we found this measurement unreliable in view of the individual variation in degree of dorsal curvature—although Hartmann (1928) used this procedure in his studies on the *Opossum*.

Our graphs (text-figs. 1, 2) follow very closely the corresponding chart given by Hartmann of the weight increments in *Didelphis*. The agreement not only applies to the general form of the graph, but also to the detailed relationship between age and weight—the time elapse in each graph being approximately the same. There is, in fact, even less scatter of the individual examples than in Hartmann's chart, especially in reference to the data borrowed by that author from Audubon and Bachmann (1851) and Meigs (1847).

On the other hand, the third graph shows important differences from Hartmann's chart of the body-length/age ratio in *Didelphis*. His curve covers a period of ninety days and is much steeper than the growth-curve based on weight, the steepness being fairly uniform. In our chart of *Dasyurus* (text-fig. 3), based on increments in head-length, the curve is a fairly flat one, rising more abruptly in the last ten to twelve days. There is also a more abrupt increment at the

Fig. 1.



beginning. It would appear, therefore, that the head-size early attains a high percentage of the total body-length, in accordance with the general principle of advanced development of the anterior over the posterior part of the body. Thereafter the head-size remains relatively static for some six weeks to two months until the elongation of the muzzle takes place, forming then a large proportion of the total head-length.

(b) *The eruption of the teeth.*

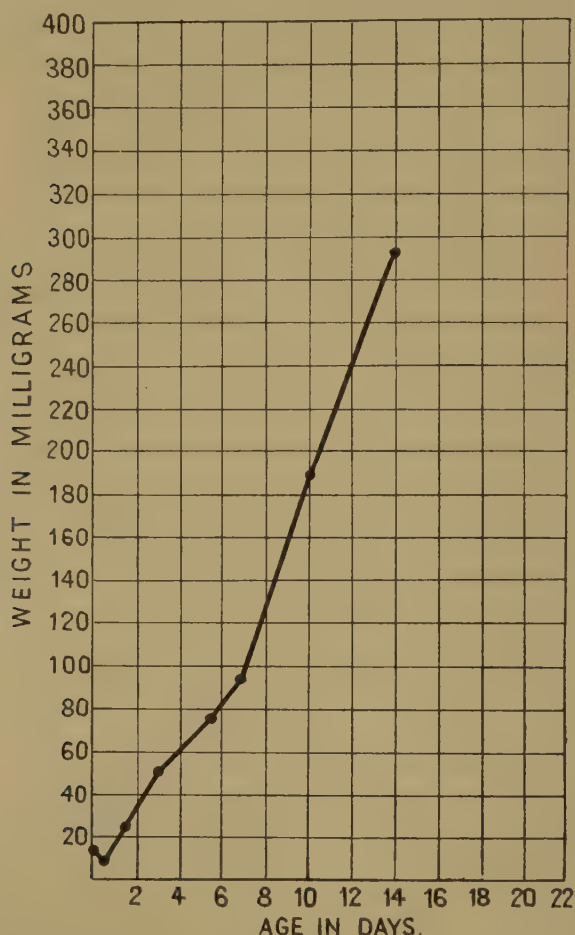
It may be recalled that the dental formula of the adult *Dasyurus* is :—

$$i. \frac{4}{3}, c. \frac{1}{1}, pm. \frac{2}{2}, m. \frac{4}{4}.$$

According to Thomas (1887), it is the hindmost tooth of the premolar series, above and below, regarded by him as [pm. 4], but by most other writers as [pm. 3], which has been suppressed. This has been confirmed by Woodward (1896, p. 286)

who records that in the pouch-young of *Dasyurus* he observed "a well developed labially situated bell-shaped enamel organ with a calcified tooth often very irregular but sometimes of considerable size, this represents the so-called deciduous fourth premolar [dpm. 3], whilst lingually the dental lamina is much swollen" and seems to represent "the so-called permanent 4th premolar dpm. 4" [pm. 3], though it probably does not differentiate much further. There is no evidence that the vestigial [dpm. 3] ever erupts.

Fig. 2.



Weight increments in *Dasyurus* pouch-young for the first 14 days.

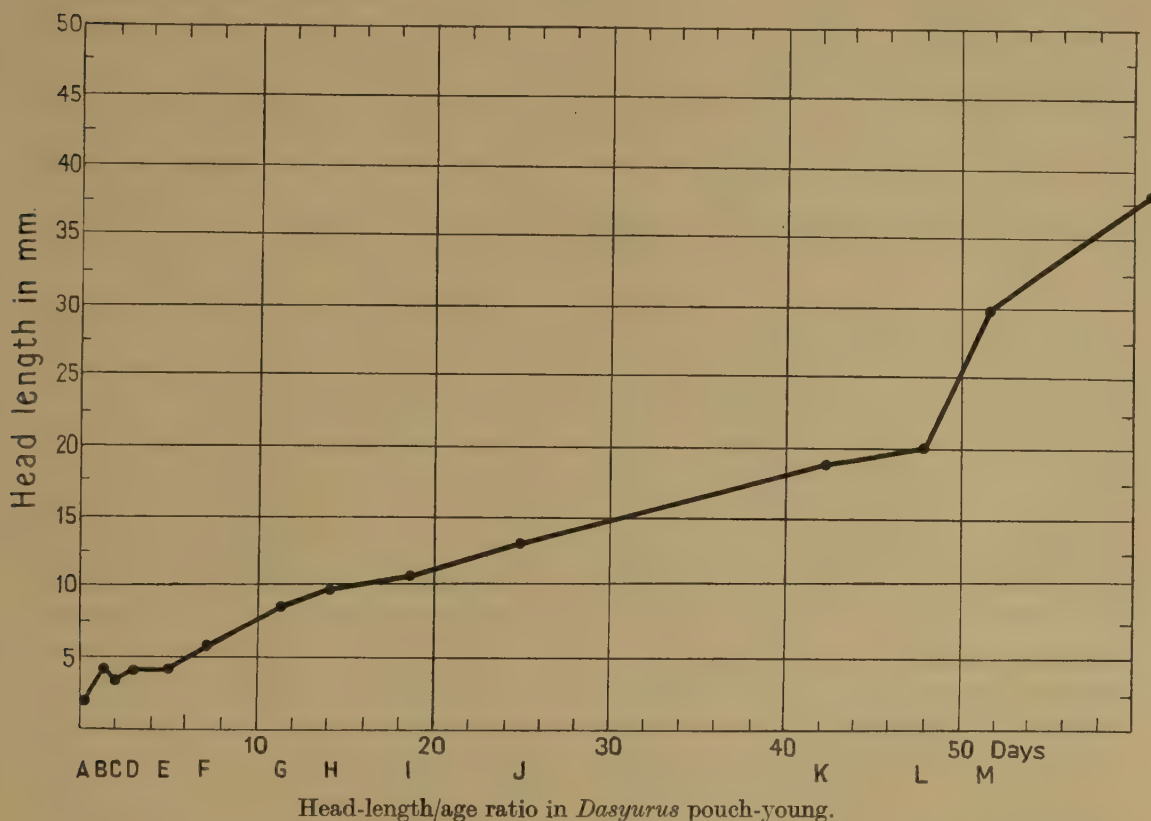
First indications of teeth about to erupt are observed in stage M, where the gums are marked by rounded hillocks caused by the underlying teeth. In the upper-jaw the premaxillary area is flat, except for the median papilla palatina. The region destined to be occupied by the cheek-teeth is marked by a narrow ridge of thickened epithelium (Zahnwall of German authors) running antero-posteriorly parallel with its fellow of the opposite side. Its anterior end is marked by two minute hillocks. In the lower jaw three or four small rounded prominences are found on each side at the front of the jaw, the hindmost being rather indefinite.

In stage N a single incisor (i_2) is commencing eruption in the upper jaw, level with the lateral limit of the philtrum. Below, three incisor tips (i_{1-3}) are recogniz-

able, the median being largest, antero-posteriorly flattened and shaped like a truncated cone in frontal view. Lateral to it are two small conical incisor apices emerging through the gum. No cheek-teeth are as yet in view.

In a specimen between stages N and O, with head-length 42.5 mm. there is no advance on the above in the upper jaw, though the tip of a single cheek-tooth (pm.^1) is palpable through the gum at the anterior end of the muco-periosteal ridge. In the lower jaw the three incisors are slightly further advanced, and the tip of the foremost cheek-tooth (pm._7) is showing through the gum.

Fig. 3.

Head-length/age ratio in *Dasyurus* pouch-young.

In pouch-young a week, or slightly more, older than stage O, with a head-length 51.5 mm., two upper lateral incisors are well erupted and the canines are partially in view, as well as the foremost cheek-tooth (pm.^1). The lower jaw shows no advance on the preceding stage. There is evidently some variation between litters (all members of one litter seem to be alike), for in a stage between O and P, with head-length 48–50 mm., there is a great advance on the stage corresponding to O. The dental formula in this particular litter is $i. \frac{4}{3}$, $c. \frac{1}{1}$, $\text{pm.} \frac{2}{2}$, $m. \frac{2}{3}$. The anterior cheek-teeth ($\text{pm.} \frac{2}{2}$) both above and below are very small, as is also the upper central incisor ($i. \frac{1}{1}$) which has now appeared.

Eleven days later than the pouch-young of 51.5 mm. head-length (i.e. with head-length 58 mm.) the upper canine crown measures 1.5 mm. long. All the incisors are well erupted.

At fifteen weeks the pouch-young will feed on meat of their own accord. Two days later they have a head-length of 63 mm. and, in the particular litter examined the upper central incisors ($i.1$) were coming through, with the three outer ones ($i.2-4$) much more advanced. Only after another nine days is the central incisor ($i.1$) well advanced in this group, the head-length being now 64.5 mm.

At four months old (stage P), i.e. eleven days older than the stage just mentioned, the pouch-young is a replica of the adult and behaves as such, biting savagely when approached. The dentition is now well erupted, except that the hinder two upper ($m.3-4$) and the hindmost lower cheek teeth ($m.4$) have not yet appeared and must evidently await the elongation of the jaws to enable them to accommodate themselves. The hindmost upper cheek-tooth erupted ($m.2$) is represented by the apex of its principal cusp only.

The curious retardation in the appearance of the upper median incisors, noted above, was observed by Thomas (1887, p. 453) who states that it occurs in all the three Polyprotodont families.

Apart from the absence of [dpm. 3] and its successor (pm. 3), tooth-eruption in *Dasyurus* does not appear to differ essentially from that in *Perameles* or *Didelphis*.

In *Perameles*, Wilson & Hill (1897) state that in their stage IX (head-length 40 mm.) the deciduous premolars (dpm. 3) have cut the gum and project slightly, in stage X (head-length 50 mm.) they are only just cutting the gum, whilst in the lower jaw, in addition $i.1-2$ have erupted and $i.3$ is in process of eruption. In stage XII (skull-length 56 mm.) all the antemolar teeth except pm. $\frac{3}{3}$ have cut the gum and $m.1-2$ and $m.1-3$ have erupted.

According to McCrady (*loc. cit.*, pp. 201-2) the first tooth in *Didelphis* to erupt is the deciduous third premolar, as in *Perameles*. It does not appear until the age of sixty days, and is shed between the ninetieth and three hundredth day and replaced by the permanent premolar. The second tooth to erupt is the second premolar at seventy-five days. The hindmost four incisors, canines and foremost premolar follow between the seventy-fifth and eighty-fifth days. In another ten days first molars and first incisors are present, leaving the third premolar and last three molars to be erupted.

PART 2.

OBSERVATIONS ON THE ANATOMY OF THE NEW-BORN YOUNG.

INTRODUCTION.

As is well known, the Marsupialia have the distinction of bringing forth their young in a much more immature condition than is the case in any other mammalian Order, not excepting the Monotremata, the new-born young of *Dasyurus* being in this respect more embryonic in its structural organization taken as a whole, than any other new-born marsupial hitherto examined.

But it is not so generally realized how great is the adaptive specialization that the new-born marsupial exhibits. From the very start of embryonal formation, the developmental processes are directed to the production of an embryo, possessed of the minimum organization necessary for its free existence but remarkably well equipped with those organs and structures which will enable it to find and gain attachment to the nipple and so obtain the sustenance necessary for its existence.

Except in a few pouchless species, the nipples are located in the pouch or marsupium and in this the young, firmly attached to the nipples, remain until they are far enough advanced to live a free life on their own and even after that, they may utilize the pouch to procure additional nutriment and as a haven of refuge.

It is often assumed that the immature condition of the new-born marsupial is directly related to, if not induced by this pouch habitat, but theoretical considerations apart, such evidence as we possess negates any such idea. The extensive investigations of Bresslau (1912, 1920, pp. 80–81) on the mammary apparatus led him to the conclusion that the pouch has been evolved within the limits of the Marsupialia and that the ancestral marsupials, like the existing didelphids, *Monodelphis* (*Peramys*) *henseli* and *Marmosa pusilla* lacked a pouch (Thomas, 1888, figs. 6 and 8, Pl. XXVIII; Bresslau, 1912, fig. 6, p. 671). Unfortunately we have no knowledge of the new-born young of these pouchless species but in the absence of evidence to the contrary, we may assume they resemble in all essential respects, those of the pouched marsupials.

Nevertheless, it is clear that quite a number of the structural peculiarities of the new-born marsupial are adaptive in significance and have been evolved to enable it to cope with the unique conditions in which it is destined to live during the early part of its existence. We need only instance the powerfully developed fore-limbs, adapted for crawling and hanging on to the hairs of the mother, which enable it to reach the nipple; the sucking mouth adapted for grasping hold of the same and the adaptations which enable it to breathe and feed simultaneously during the relatively long period it is firmly attached thereto.

There would appear to be two factors which have profoundly influenced the organization of the new-born marsupial, (1) the short period of gestation, to which is to be attributed its immature condition and (2) the necessity of feeding itself, a necessity which involves, primarily, the possession of means whereby it can reach the nipples and secondarily, the possession of structural adaptations which will enable it to suck the nipple into its buccal cavity and retain it there until such time as it has advanced enough to be able to lead a free life, a condition, obviously, of the highest survival value.*

As regards the length of the gestation period, that is known with a high degree of accuracy in the case of *Didelphis*. Selenka (1887) concluded that birth took place twelve days, twenty-one to twenty-two hours after coition. Hartman (1928) with wider experience of breeding Opossums than Selenka, considered "thirteen days is probably near the truth for the average period from copulation to birth: twelve and one-half days for the actual prenatal development" (p. 187), whilst McCrady (1938) states, "all the evidence points to a sharply defined gestation period of about $12\frac{3}{4}$ days" (p. 175).

Owen (1834), from observations on a female Kangaroo (*M. major*) in the Gardens of the Zoological Society, concluded that the gestation period in this species is

* Since the above paragraph was written, we find that Leche (1890) had expressed much the same view. He writes (page 116), "Diese Thatsachen berechtigen also zu der Auffassung, dass die Beuteltiere, abweichend von allen andern Amnioten ein wirkliches Larvenstadium mit provisorischen Organen durchlaufen, welches Stadium theils durch die Kürze des Embryonallebens, theils durch die eigenartigen Existenzbedingungen während des Aufenthaltes im Marsupium, respective während der Säugeperiode hervorgerufen wird". But we cannot subscribe to his conception of the new-born marsupial as a real larval stage.

thirty-eight days. Copulation was observed on the 27th August and after some hours, the male was removed and not again admitted to the enclosure. On the 5th October at 7 a.m., the thirty-ninth day, a young one, measuring "one inch from the mouth to the root of the tail", was found attached to the left superior nipple. It was not there when the pouch was examined on the preceding day and so must have been born during the night. Harrison Matthews (1943) in his paper on the parturition of the kangaroo also states that the new-born young one "was about an inch long". Although a gestation period of thirty-eight days appears long by comparison with that of the Opossum, the evidence presented by Owen is unequivocal and it must be remembered that *M. major* is the largest of living marsupials and we do not know whether coition and ovulation are coincident or nearly so or are separated by an interval as in *Dasyurus* in which it may reach an observed maximum of eight days.

In this connection, it is perhaps worth recording that Ben Ford, a highly intelligent bushman and an acute observer informed us in 1896 that he had kept Pademelons (*Thylogale thetis*) in captivity and that the young are born twenty to twenty-five days after coition.

Comparison of the new-born young of *Dasyurus* with uterine stages and the new-born young of *Didelphis* and assuming that the developmental rate is approximately the same in the two genera, suggests that the gestation period in *Dasyurus* is a day or two less than that of the Opossum, possibly about eleven days. The same estimate was arrived at by Hill & O'Donoghue (1913, p. 150) on other grounds. From our present point of view, one of the most interesting results arising from the series of hemi-hysterectomies (removal first of one pregnant uterus, and then the other after a known period of time), carried out by Dr. Hartman (1928) is his demonstration (clearly set forth in his chart, text-fig. C, pp. 148-149), that at seven and a half days, the primitive streak is completed, the medullary plate is beginning to differentiate and the notochord is beginning to grow forwards from Hensen's node. Reckoning the gestation period as being about thirteen days, that leaves only about five and a half days for the actual development of the embryo itself to the time of birth (p. 173).

In that short space of time, during which the developmental rate must be strikingly increased, all the embryo can do (and it is a remarkable achievement) is to concentrate on providing itself, on the one hand, with the minimum organization which will suffice for its bare existence when born and on the other, with those structural adaptations which are essential (1) for the procuring of the milk on which its continued existence depends and (2) for its survival, dependent as it is on a mother, seemingly devoid of all but the rudiments of the maternal instincts. Beyond supplying the milk, all that the marsupial mother does for her young is to clean out the pouch, in preparation for their arrival, to lick the median tract of hair intervening between the cloacal aperture and the pouch so as to leave a smooth and moist path along which they can crawl to the latter (McCrady, *loc. cit.*; Matthews 1943)* and to lick them clean as they emerge into the world (Hartman, 1920).

* This paper in addition to providing new observations on parturition in the kangaroo, contains an excellent summary of the literature relating thereto.

These considerations go some way towards an understanding of how the remarkable combination of immaturity and advanced specialization, which the new-born marsupial exhibits, has come about. But we still lack the data on which to base an adequate explanation of why parturition should occur in the marsupials after such a short period of gestation. Meantime Amoroso (1949) has made the interesting suggestion that the marsupials, with their relatively simple placental arrangements, have not yet evolved the endocrine secretions which, in the Eutheria, are furnished by the placenta and control the gestation period, enabling it to be lengthened for so long as may be necessary. Definite evidence confirmatory or otherwise of this suggestion is highly desirable.

Amongst the structural features characteristic of the new-born *Dasyurus* (most of them of an adaptive nature and occurring also in other new-born marsupials) are the following :

1. The relatively enormous development of the fore-limbs and their musculature as compared with the hind-limbs in which there is neither skeleton nor musculature. The presence on the digits of the manus (except the 1st) of sharp, recurved "larval" claws, capable of being flexed and extended and so of grasping hold of the hairs of the mother and which are deciduous, being shed shortly after the young one has firmly attached itself to the nipple.

2. The almost completely developed condition of the voluntary muscular system (except for that of the pelvic region, hind-limbs and tail), capable of functioning, its muscle fibres, though embryonic in having their nuclei central, being striate. Indeed, they are already striate in uterine stage ϵ .

3. The small, triangular-shaped mouth, surrounded by an "oral shield", adapted for sucking on to the nipple and for its subsequent retention in the buccal cavity, the lips being all but completely fused laterally.

4. The large tongue, with slightly projecting tip and its musculature, both intrinsic and extrinsic, fully developed and innervated by relatively large hypoglossal nerves, the whole suggestive of an actively functional organ, possibly capable of a suction-pump-like action.

5. The large, intra-pharyngeal epiglottis, the termination of the soft palate in a dorso-ventrally expanded lamina, against which the epiglottis would appear to be applied and the well-developed palato-pharyngeal folds, together forming parts of a structural arrangement, which permits breathing and the swallowing of the milk to go on simultaneously.

6. The presence in the new-born *Dasyurus* and only in it so far as known, of a bladder-like "cervical" swelling to support the head and keep it more or less at right angles to the trunk, thus facilitating the application of the mouth to the nipple.

7. The presence over the very thin epidermis of an impermeable keratinized membrane, the epitrichium, for the protection of the young one from desiccation, whilst crawling from the cloacal opening to the pouch.

8. The advanced condition of the olfactory apparatus, in marked contrast with the eye and ear which are still in an embryonic condition. Olfactory sense cells are present in the olfactory epithelium and the olfactory bulbs are relatively large,

receive bundles of olfactory nerve fibrillae and have attained a fair degree of differentiation. Thus the new-born probably possesses in some degree the sense of smell and the distribution of the terminal branches of the divisions of the Vth nerve suggests that it is probably also capable of responding to tactile stimuli.

9. In the brain, apart from the presence of connecting tracts between the olfactory bulbs and the medulla, the fore- and mid-brains have advanced but little beyond the embryonic condition, the cerebral hemispheres having the form of simple, relatively thin-walled vesicles. But the medulla oblongata and the cervical and thoracic regions of the spinal cord attain a fairly high degree of differentiation, whilst the cranial ganglia and nerves and the cervical and thoracic spinal ganglia and nerves are well established.

The new-born marsupial thus possesses a neural organization sufficiently advanced to enable it to carry out the complex reflex activities which alone it is capable of displaying.

EXTERNAL CHARACTERS.

(a) *Oral shield.*

From the figure of the new-born young, stage A (Pl. 1, fig. 2), it will be seen that the triangular mouth-opening from which the tip of the tongue projects, is bounded laterally by two curved thickenings which, separated by a slight median groove, converge dorsally to form the tip of the snout and at the same time, the anterior boundaries of the external nares. Behind that, as is clearly seen in fig. 1 of uterine stage η , they are continued back on each side, dorsally to the external naris and the eye-primordium as a distinct supra-orbital ridge which terminates above the external auditory meatus. Below the mouth-opening, in the position of the lower lip is a well-marked transverse thickening, slightly arc-shaped, which, at its outer end, is separated on each side from the corresponding lateral thickening by a slight transverse groove. This latter is really the opening of a quite narrow slit which continues back between the lips for a very short distance so that in the new-born still unattached young, lip fusion is not yet quite complete. The two lateral thickenings and the ventral thickening together form the so-called oral shield.

This curious formation was first described and figured by Selenka (*loc. cit.*) in the Opossum where it is even more conspicuous, under the name of the "Schnabelschild" (see especially his beautiful fig. 5, and also figs. 4 and 6, Taf. XXVII, illustrating its appearance in the late uterine embryo). In the fully formed condition, he describes it (p. 157) as surrounding the mouth-opening like a flat collar which is produced marginally into six projections, of which the most ventral pair, on the lower lip, is sharp pointed. He states that already some hours before birth, it appears distinctly degenerate and that in the new-born young, only a slight remnant of it is recognizable. In attempting to explain its significance, Selenka came to the conclusion that it is the vestige of a horny bill comparable with that of *Platypus* which served as a grasping organ in the ancestors of the Opossum!

McCradly (*loc. cit.*) quotes this altogether fantastic view without comment and himself refers to the oral shield as "this apparently useless organ" (p. 168). In agreement with Selenka, he further states that in his stage 35 which includes young very shortly before and immediately after birth, the oral shield has suffered "almost complete resorption" (p. 172).

On the other hand, Dr. Carl Hartman has informed us that it is still present in the new-born young and we ourselves have photographic records of its existence in new-born specimens he was good enough to send us in 1917.

Our own suggestion as to the functional significance of this unique formation is that it is an adaptive device which, when the flat oral region is applied to the minute nipple, comes into contact with surrounding skin-area and acting as a more or less air-tight washer, enables the young one the more easily to suck the nipple into its buccal cavity.

In short, we suggest it is analogous to the rim of the sucker of a cephalopod. It is clear that the new-born marsupial must be capable of suction for by no other means could the nipple be drawn into the buccal cavity. Hartman (1920) indeed observed the new-born young of the Opossum, in the pouch, "engaged in very active respiratory and sucking movements" (p. 5) and McCradly (*loc. cit.*) states that they "can be seen and heard to suck" (p. 188). But just how suction is effected is by no means so obvious. Is it purely inspiratory or due to the tongue with its powerfully developed musculature acting as a kind of suction-pump by alternately retracting and relaxing or to a combination of the two? We have no definite answer and can only suggest that the tongue is probably more efficient in producing a negative pressure in the buccal cavity than is the diaphragm (*v.* Feldman (1920) for a discussion of the mechanism of sucking in the human infant).

Both Selenka (*loc. cit.* p. 157) and McCradly (*loc. cit.* p. 168) state that the shield in the Opossum is formed of cornified epidermal cells. This is certainly not the case in that of *Dasyurus*. Over the body generally, the epidermis is extremely thin, being composed of a single layer of cells, surmounted by the thin completely keratinized membrane, forming the epitrichium and containing sparse degenerate and greatly flattened nuclei. The epidermis of the shield on the other hand has the structure of a thick stratified epithelium (Pl. 3, fig. 18, *ep. os.*). Over the lateral segments of the shield it is composed of a basal Malpighian layer of small, more or less cubical cells, surmounted by one or two layers of flattened cells, outside which are large, oval, vesicular cells with distinct limiting membranes and centrally or peripherally situated nuclei and arranged two to three deep. They exhibit no trace of keratinization. The superficial epitrichium is thick over the upper portions of the segments but becomes distinctly thinner below. The epidermis attains a maximum thickness of about 0.055 mm. (in long series stage A). That of the lower lip segment is similar in structure but is much thicker (reaching about 0.13 mm.), owing to the increase in number and size of the vesicular cells, but the epitrichial layer covering it is very thin.

The existence of an oral shield has so far been observed only in *Didelphis* and *Dasyurus*. It is certainly not obvious as a demarcated formation in the new-born

young of *Perameles* or in those of *Trichosurus*, *Macropus* and *Phascogale*. But the margins of the upper and lower lips bounding the mouth-opening appear distinctly tumid and sections show that they are covered by a greatly thickened epidermis, recalling that of the oral shield. In all these forms, it should be remembered, the new-born young are larger and altogether sturdier and more massively built than those of the Opossum and Native Cat and so presumably are better endowed with suction capacity than are the latter and at the same time more capable of bringing the circum-oral region of the snout forcibly into intimate and firm contact with the skin-area around the nipple, so that an organized oral shield is not so necessary.

Another noteworthy feature in the snout of the new-born is provided by the presence of two very large groups of sinusoidal-like capillaries situated immediately above and laterally to the dorsal angle of the mouth and directly behind the epidermis of the oral shield (Pl. 3, fig. 18, *cp.*).

Below the prenasal laminae, they occupy the space between them and the roof of the buccal cavity and extend out laterally into the lateral segments of the oral shield. Slightly more posteriorly, below the ventral wings of these laminae, the capillary bed forms a broad transverse band (0.56 mm. wide and 0.18 mm. thick in series 5.10.VII.02) which rapidly becomes reduced and resolves itself into a small number of normal capillaries. Figure 19, Pl. 3 of an oblique horizontal section passing through the external nares shows the two groups of capillaries in question (*cp.*) but at this level gives but a poor idea of their extent. In the lower jaw, immediately behind the upper part of the oral shield, a few enlarged capillaries are present but reach nothing like the dimensions and extent of those in the snout. These capillaries would seem to provide a soft, cushion-like bed for the oral shield epidermis.

(b) *Cervical swelling.* (Pl. 1, figs. 1-4; Pl. 3, fig. 20, *cs.*)

This remarkable bladder-like structure has been observed so far only in *Dasyurus* (Hill, 1900). It reaches its maximum size in the new-born and thereafter gradually becomes reduced and disappears. It lies between the fore-limbs, being attached to the thoracic wall in front of the sternum and to the neck region and under-surface of the head. Histologically it consists of a fairly uniform mass of delicate, embryonic connective tissue continuous with the denser tissue investing the ventral surface of the sternum and containing capillaries in variable numbers.

Its function, we suggest, is to act as a supporting cushion to the head, which keeps the latter more or less at right angles to the trunk and so facilitates the application of the mouth to the nipple. The new-born young of other marsupials available for examination would seem to be sturdy enough to be able to keep their heads up without such a support.

(c) *Claws.* (Pl. 1, figs. 2-5; Pls. 3, 4, figs. 24-26, *dc.*)

The sharp-pointed recurved claws with which digits 2-5 of the manus of the new-born young are provided were termed "larval claws" (Hill, 1900) to emphasize the fact that they are temporary structures destined to be shed by the

time the pouch-young reach stage D (about three days' old). "Deciduous" is a more appropriate designation for them. But temporary though they be, they are structures of great adaptive interest and of outstanding importance to the new-born young.

Their function, as Hartman (1920) and McCrady (*loc. cit.* p. 183) have observed in the living new-born Opossum is to enable the digits of the hand to grasp firm hold of the hairs on the ventral abdominal wall of the mother as the young one crawls, by means of the alternate over-arm movements of its fore-limbs, from the cloacal opening to the pouch. Once in the pouch, by grasping the hairs lining it, they enable the young one to crawl about, in order to locate a nipple and once the mouth of the young one has made contact with the latter, by grasping the hairs around it, they keep the young one in place whilst the nipple is being drawn into the buccal cavity (*cf.* Beard 1897, p. 87; and Langworthy, 1928).

The presence of sharp claws on the fingers of the new-born Opossum and their grasping capacity appears to have been first described by Dr. B. S. Barton in his letter on the Generation of the Opossum published in 1806 and reprinted in 1823, from which a long extract is quoted by Owen in his article on the Marsupialia in Todd's *Cyclopaedia*. Dr. Barton writes (p. 352 of reprint): "The toes of the fore-foot of the new-born embryo opossum are furnished with sharp and hard nails or claws but this is not the case with the hind-feet. The latter are for some weeks of little use to the animal; but by means of the former it is enabled to cling most firmly to the teat; and especially to the hair in the marsupium immediately around the teat".

That the grasping of the hairs around the nipple continues energetically for some time after fixation to the latter has been effected, is convincingly shown in the film taken by Prof. L. S. Stone to illustrate the life-history of the pouch-young Opossum. Dr. R. Broom (quoted in Beard, 1897, p. 87) observed that the pouch-young of *Trichosurus* when removed from the nipple, also makes constant "clawing" movements with the fore-limbs. One is tempted to wonder if this persistent tugging of the hairs around the nipple may not have some stimulatory effect on the flow of the milk.

Furthermore, in view of the fact, first observed by Hartman (1920) and later confirmed by McCrady (*loc. cit.*) that the uterine embryo of the Opossum, if removed from the uterus and its membranes, shortly before birth, is capable of crawling, it may be suggested that the claws are of service to the young one during parturition in tearing through the foetal membranes, especially in making for itself the irregular slit-like passage (the pseudo-vaginal passage) in the connective tissue intervening between the lower end of the median vagina and the uro-genital sinus. The first-born of the litter is the pioneer, its litter-mates have but to follow in its track, perhaps a less difficult but still a not too easy task.

The larval claws are simply thickened prolongations of the epitrichium. Longitudinal sections through the digit show that the phalangeal joints are not yet formed and that the terminal phalangeal procartilage gradually thins to terminate in a blunt extremity, situated shortly behind the tip of the digit and is slightly bent ventrally (Pl. 4, fig. 24; Pl. 5, fig. 25, *ph.c.*).

The epidermis on the dorsal surface of the digit begins to thicken some distance back from the tip, becoming two layers thick and reaching its maximum over and round the tip of the phalangeal procartilage. The epitrichium also thickens and, beyond the epidermis covering the tip of the digit, is prolonged to form the slender, recurved, sharp-pointed claw which is joined at its base by the thinner epitrichium on the ventral surface of the digit. It is refractive, being strongly keratinized, exhibits slight indications of lamination and its nuclei are reduced to mere traces (Pl. 4, fig. 24, *dc.*).

The claws are controlled by well-developed flexor and extensor muscles. There is a single ventral flexor muscle, short and thick and relatively massive (figs. 24, 25, *fl.m.*). It terminates in a broad, thick tendon (*fl.t.*) which divides into four tendinous slips which run below the phalangeal procartilages of the second to fifth digits and thinning out below the terminal portions of the procartilages, appear to be inserted into the thickened epidermis at the tips of the digits. When the flexor muscle contracts, the terminal portions of the digits, including the terminal portions of the phalangeal procartilages, become sharply bent round vertically so that the tips of the recurved claws are brought into contact with the ventral (palmar) surface of the manus (Pl. 5, fig. 26). The claws thus enable the manus to grasp firm hold of the hairs of the mother.

The dorsal extensor muscle is also single though it may be subdivided unequally into two. It gives origin to a broad and rather thin tendon (figs. 24, 25, *ext.t.*) which divides into four long and slender slips, which run above the phalangeal procartilages, close below the epidermis and terminate in elongated insertions on the prospective perichondrium clothing the dorsal surfaces of the terminal phalanges, with reach within a short distance of their tips. In longitudinal section stage B, the muscle also possesses an accessory tendinous insertion on the dorsal surface of the proximal end of the middle phalangeal procartilage of one of the middle digits.

As regards the occurrence of larval claws in other marsupials, Hartman (1928, 1952, p. 113) has confirmed Dr. Barton's observation of the presence of claws on the fingers of the new-born Opossum, stating that they are deciduous and McCrady (1938) calls attention to their presence in his Stage 34, shortly before birth (Pl. 3, fig. 34). We ourselves have figured them in the new-born *Perameles nasuta* (G.L. 14 mm., H.L. 6 mm.) (Hill, 1897, Pl. 33, fig. 36) where they are present as the second to the fourth digits, though not at that time recognized as "larval" and our records under date 18.VII.05, show that they are also present in the recently born young of *Isodon obesulus* (*P. obesula*) (G.L. 14.25 mm., H.L. 6 mm.) but have been shed in the pouch-young of the same species measuring in G.L. 15 mm. and H.L. 7.5 mm. In a recent paper, Lyne (1952) also records the presence of deciduous claws on the second to fourth digits of the manus of *Perameles gunnii* and *Isodon obesulus*.

Strongly developed recurved claws are present on all the five digits of the manus of recently born young and uterine embryos shortly before birth of all the diprotodont marsupials we have been able to examine (*Macropus*, *Trichosurus*, *Phascolarctos*, *Phascolomys*). Examination of sections shows that they are formed

of greatly thickened epitrichium and are therefore deciduous but we have no record of when they are shed.

BUCCAL CAVITY AND PHARYNX AND THE STRUCTURAL ADAPTATIONS
FOR BREATHING AND FEEDING.

(a) *Tongue.*

The tongue is a remarkably well-developed organ. Its intrinsic muscles are fully established as well as its chief extrinsic muscles (Edgeworth, 1935) and the hypoglossal nerves innervating them are large (Pl. 3, fig. 18; Pl. 4, figs. 22 and 23, *tg.*).

In the unattached young, the tongue narrows forwards to its bluntly rounded tip, which usually projects slightly through the oral opening. Its surface is smooth and over its apical region it is not grooved* but slightly convex, more posteriorly. It becomes shallow saucer-shaped in section and finally flat over its basal region. In series B3 (unattached), it has a length of about 0.60 mm. its apical portion being free over a length of 0.25 mm.

Consequent on the drawing of the nipple into the buccal cavity, its anterior portion becomes grooved and assumes the characteristic semi-tubular form, partially enclosing the nipple, well seen in Pl. 4, fig. 23 from stage D.

The advanced state of organization of the tongue suggests that it is of more functional importance to the new-born young than has been suspected hitherto. Largely filling as it does the posterior portion of the buccal cavity (Pl. 4, fig. 22, *tg.*) may it not be that, once the oral shield has become applied to the skin-area around the nipple, it exerts a suction-pump-like action and, by its alternate retraction and relaxation, helps to draw the nipple into the buccal cavity?

(b) *Larynx.*

The development of the laryngeal cartilages has been described and figured from models by Esdaile (1916) in pouch-young of *Perameles* from a stage of *P. obesula* (G.L. 15.5 mm.), a day or two after birth to a pouch-young of *P. nasuta* (H.L. 35 mm.), whilst Edgeworth (1935) has provided figures of seven sections showing the hyoid, larynx and related muscles in *Dasyurus*, stage A (figs. 708 *a-g*, and p. 177).

Symington (1899) amongst others (see his paper for references), has described the anatomy of the larynx in pouch-young of *Macropus* and in various adults.

The laryngeal cartilages in the marsupial are secondarily modified in as much as the body of the thyroid cartilage and its posterior cornua are fused with the cricoid cartilage, whilst the posterior cornua of the hyoid bone pass back to fuse with the thyroid cartilage laterally, those parts thus forming a connected cartilaginous framework, the arytenoids alone remaining separate from it. According to Symington (*loc. cit.* p. 35), Gegenbaur pointed out that this condition renders the larynx a more efficient support for the epiglottis, but whilst accepting this, he himself suggests that the cause of this fusion is to be associated with the rudimentary condition of the vocal cords, a large number of the marsupials (but certainly not including the Thylacine and the Native Bear), being voiceless.

* In late uterine embryos of other marsupials (e.g. *Trichosurus vulpecula*), the projecting tongue is distinctly grooved.

Symington (p. 38) states that in marsupials, an interarytenoid cartilage "seems to be regularly present" but Esdaile failed to find it in *Perameles* and we have failed to recognize it in the new-born *Dasyurus*, though Edgeworth figures it in stage D (his fig. 709).

In the new-born *Dasyurus*, the laryngeal cartilages are in a much earlier developmental condition than in the earliest stage described by Esdaile, since the thyroid cartilage is still paired and distinct from the cricoid and the posterior cornua of the hyoid still end freely.

The glottis (aditus laryngis), bounded by the upstanding epiglottic folds, is funnel-shaped in section. It is wide in front and gradually narrows backwards, its total length in series 5.10.VII.02 being 0.07 mm. (Pl. 3, fig. 21; Pl. 4, fig. 22; Pl. 6, fig. 29, *gl.*). The laryngeal cavity (*l.c.*) is relatively large and there is a trace of the laryngeal recess which occurs in many marsupials (cf. Symington, *loc. cit.* pp. 35-36).

The thyroid cartilage, as just noted, is paired, being represented by two small obliquely disposed cartilages, situated in the base of the epiglottis, immediately behind and dorsally to the basihyal (Pl. 5, fig. 28, *th.c.*). They have a vertical height of about 0.17 mm. and are continued back as two laterally situated, slender, rod-like cornua, with a length of about 0.22 mm. (fig. 29), which terminate freely, shortly in front of the division of the cricoid cartilage into its two cornua (Pl. 6, fig. 29, *c.th.* also Pl. 4, fig. 22, *c.th.*).

The cricoid (Pl. 6, fig. 29, *cr.c.*) is by far the largest of the laryngeal cartilages. Its anterior segment underlying the aditus laryngis and the laryngeal cavity takes the form of a transverse curved bar, which becoming horse-shoe shaped, supports the arytenoid cartilages. Then, through the thinning out of its mid-ventral portion, it becomes reduced to two lateral bars and these, behind the arytenoids, unite dorsal to the laryngeal cavity to form a second horse-shoe shaped segment, connected below the latter by a thin layer of cells not yet procartilaginous in series B3 but definitely so in series 5, 20.10.VII.02, so that the cricoid surrounds the laryngeal cavity ring-like. The thicker dorsal portion of the cricoid finally separates into two short cornua (0.064 mm. in length in series B3), lying dorso-laterally, between the oesophagus and the trachea, now supported by the tracheal cartilages.

The arytenoid cartilages (Pl. 6, fig. 29, *a.c.*) situated in the bases of the epiglottic folds, bounding the aditus laryngis and resting on the lateral limbs of the cricoid, are short and rod-like (with a vertical thickness of about 0.10 mm. and a total length of about 0.11 mm. in series 5.10.VII.02). Behind the glottis, their upper ends come into close apposition in the middle line and fuse as seems to be the case also in *Perameles* (Esdaile, *loc. cit.* p. 450).

(c) *Epiglottis.*

The epiglottis, seen in median longitudinal section (Pl. 3, fig. 21; Pl. 4, fig. 22, *epg.*) appears as a relatively large conical structure which projects upwards and slightly forwards into the pharyngeal cavity, immediately behind the expanded free margin of the velum palati. The upper portion of its anterior surface is slightly convex, whilst the thickened posterior margin of the velum palati is

concave and is produced down into a thin tapering lamina which projects into the well-marked transverse groove (figs. 21, 22, *gep.s.*) situated between the base of the tongue and that of the epiglottis (the glosso-epiglottic sulcus). From the configuration of the parts, it seems highly probable, indeed it would appear to be essential that during life, the convex anterior surface of the epiglottis lies in close apposition with the concave posterior margin of the velum palati, a relationship of great functional significance, as we shall point out below.

Seen in transverse section (Pl. 5, fig. 28, *epg.*), the epiglottis appears as a truncated cone, with sloping sides and a flat top which becomes grooved posteriorly, the groove leading into the glottis (aditus laryngis). It is bounded at its base, on each side, by a distinct groove, the laryngo-pharyngeal groove (*lp.gr.*). These grooves are continuous with the glosso-epiglottic sulcus in front; they continue back alongside the glottis which is situated well above them and behind that, continue along the posterior prolongation of the pharynx and so finally merge into the lumen of the oesophagus.

Projecting down from the lateral pharyngeal wall into the laryngo-pharyngeal grooves are two distinct folds, the palato-pharyngeal folds (figs. 28, 29, *pp.f.*), the functional significance of which in the marsupial was first emphasized by Symington (*loc. cit.* p. 32). The folds take origin in front at the level of the posterior margin of the velum palati and are continuous with its lateral attachments. They are co-extensive with the laryngo-pharyngeal grooves and extending back, finally unite on the dorsal wall of the oesophagus (figs. 21, 22, *pp.ft.*), giving to its lumen a semilunar appearance (in transverse section), before disappearing.

As Symington (*loc. cit.*, p. 32) has pointed out, the folds thus form an elongated narrow ring (the annulus or arcus palato-pharyngeus of authors) which, completed in front by the posterior margin of the velum palati, encircles the epiglottis and the glottis and ends by the union of its lateral limbs on the dorsal side of the oesophageal lumen.

As is well known, the attachment of the pouch-young marsupial to the nipple renders it essential that it should be able to respire and to feed simultaneously and to enable it to do so, special adaptations have been rendered necessary. These have been described above, in the case of the new-born *Dasyurus*.

As concerns respiration, if, as we have suggested above, the epiglottis is applied during life to the dorso-ventrally expanded posterior margin of the velum palati, then a clear and continuous passage is provided for the respiratory current of air through the external nares, the nasal sacs, the posterior narial passage, the naso-pharynx and upper part of the pharynx directly into the glottis.

It is generally stated in the literature and in text-books that the pouch-young marsupial is characterized by the possession of an "intra-narial" epiglottis.* Symington (*loc. cit.*, p. 32) states that "a well-marked intra-narial epiglottis present in pouch-specimens" of *Macropus*. McCrady (*loc. cit.*, p. 187) also accepts the intra-narial position of the epiglottis in *Didelphys* as established, stating that it "projects into the posterior nares or choanae" as it would appear to do in his fig. 56.

* For an account of the occurrence of an intra-narial epiglottis in mammals generally, see the papers of Howes (1889).

In the new-born and later pouch-young of *Dasyurus*, on the other hand, our figs. 21 and 22 demonstrate conclusively that the epiglottis is not intra-narial but intra-pharyngeal.

In the late uterine embryo of *Isoodon* (*Perameles*) *obesulus* (G.L. 12·15 mm.), the epiglottis is also intra-pharyngeal and closely resembles that of *Dasyurus* in its relations to the velum palati. The latter terminates in a flat, bevelled free margin which slopes from above downwards and backwards and projects below into the glosso-epiglottic sulcus. The epiglottis projects downwards and forwards, its anterior surface lying close to, and parallel with the flat surface of the dorso-ventrically extended margin of the velum palati, so that during life, the two surfaces could easily come into contact and so close off the glosso-epiglottic sulcus.

On the other hand, we find that in the new-born young of *Trichosurus* (G.L. 14·5 mm.) and in the late uterine embryo of *Wallabia* (*Protemnodon*) *dorsalis* (G.L. 16·5 mm.), the epiglottis is intra-narial or more precisely intra-naso-pharyngeal in position as Owen and other anatomists have maintained. In these forms, the velum palati does not terminate in an expanded free margin but curving backwards and downwards, gradually thins to terminate deep in the glosso-epiglottic sulcus, in a relatively thin rounded tip. The epiglottis projects forwards and upwards into the naso-pharynx so as to overlie the posterior position of the velum palati (Pl. 4, fig. 22 A). In these diprotodonts, the closing off of the glosso-epiglottic sulcus would seem to be effected by the contact of the anterior surface of the epiglottis with the postero-dorsal surface of the velum palati, a slight but interesting variation from the condition in the mentioned polyprotodonts but equally effective functionally.

Now as concerns the passage of the milk : the prime necessity is, of course, that the milk in its passage to the oesophagus should be prevented from entering the glottis. Examination of figs. 21 and 22 shows that, whilst the anterior portion of the tongue has assumed a semi-tubular form to accommodate the nipple, its posterior portion is unaffected and there is left a narrow passage between its upper surface and the under surface of the velum palati, along which the milk can flow and so reach the glosso-epiglottic sulcus. Provided the epiglottis is in contact with the expanded posterior margin of the velum palati, that sulcus is closed above and the only passageway left for the milk is along the lateral channels provided by the laryngo-pharyngeal grooves and it is here that the palato-pharyngeal folds become of functional significance. Symington (*loc. cit.*, p. 33) has made the suggestion, with which we are in agreement, that the milk, flowing along the groove, presses the fold against the laryngeal wall, converting it into what is practically a closed channel and so preventing any leakage of milk into the glottis.

(d) *Historical note.*

The problem discussed above and more especially the means by which the milk is prevented from entering the larynx early excited the curiosity of anatomists. Owen (1834, p. 349 ; 1841, pp. 326-327) points out that " Prof. Geoffroy first described the modification by which this purpose is effected ; and Mr. Hunter

appears to have anticipated the necessity for such a structure, for he dissected two small mammary foetuses of the Kangaroo, for the especial purpose of showing the relation of the larynx to the posterior nares ”.

Geoffroy Saint-Hilaire's observations first appeared in 1823 in his article on the Marsupialia, of which an extract under the title “ Sur la génération des Animaux à Bourse ” was published in 1824. He dissected a free pouch-young kangaroo and found that “ le larynx est terminé par un col évasé dont le pour tous se prononce en une sorte de petit bourrelet ; tout cet ensemble est introduit dans les arrières-narines : ainsi la larynx est placé sur le voile du palais ”. By this arrangement he concluded, respiration was carried on through the nose and larynx, whilst the milk flowed along a very minute passage on either side of the projecting collar of the larynx. Once the milk was swallowed, he thought the larynx descended below the soft palate. Curiously enough, Geoffroy starts out to describe the arrangement which permits respiration and feeding to go on simultaneously but ends by concluding that they are successive acts !

One of the two dissections made by John Hunter and referred to by Owen, forms Hunterian preparation No. 3769 (*Desc. and Ill. Cat. R.C.S.* Vol. V, p. 212, 1840) and is thus described by Owen : Dissection of the right half of the head of a mammary foetus of the kangaroo, showing . . . “ the pyramidal form and great development of the epiglottis, which passes into the circular posterior nares and thus defend the trachea from the entry of the milk which may be injected down the fauces of the foetus by the mammary constrictor muscle of the parent ”. In his paper of 1834 (p. 349), Owen had already dealt with this subject and provided a figure (Pl. VII, fig. 13) of a dissection of the head of a pouch-young Kangaroo, in which the epiglottis is shown, drawn out from its position in the posterior nares. In virtue of this position, he concluded that the air-passage is completely separated from the fauces and the injected milk passes in a divided stream on either side of the cone-shaped larynx into the oesophagus.

It is thus evident that the older anatomists had already made out the main facts concerning the structural arrangements which permitted the pouch-young marsupial to breathe and feed simultaneously. All we have been able to do is to confirm and in some small degree extend their observations.

RESPIRATORY ORGANS.

(a) *Lungs.*

The lungs in the new-born *Dasyurus* are remarkably simple organs, being structurally at the lowest level compatible with some degree of functional efficiency. They take the form of thin-walled sacs, with correspondingly spacious cavities, lined by an epithelial layer and carrying capillaries in their walls. They are thus entirely devoid of the normal constituents of the mammalian lung, *i.e.* bronchioles, alveolar ducts and alveoli and in the unattached young show only the beginnings of the peripherally situated air or respiratory chambers characteristic of the lungs of later stages.

As in the adult, the lungs are markedly asymmetrical, the right lung being larger than the left, owing to the oblique inclination of the heart upwards and to the left side as Owen (1841, p. 310) long ago pointed out. They are produced forwards, in front of the openings of the prospective primary bronchi, into short apical prolongations. The mediastinal septum is complete and when fully expanded, the lungs largely fill the pleural cavities.

The trachea is supported by procartilaginous "rings", incomplete dorsally. Towards its posterior end, it increases markedly in transverse diameter to form the incipient bronchi which open into the lungs shortly behind their apical prolongations. The openings which are extensive, may be situated approximately at the same level or as appears to be more usual, that into the right lung lies well in front of that into the left. In either case there is formed what appears as a large "common pulmonary cavity" (Pl. 6, fig. 30), the middle portion of which we may regard as formed by the cavities of the primary bronchi and the lateral portions by those of the lungs. It eventually becomes subdivided by the formation of the median mediastinal septum into the large right and the smaller left lungs (Pl. 6, fig. 31, *rl.*, *ll.*).

The walls of the lungs are composed of the lining respiratory epithelium in the form of a single layer of low cubical or in places, flattened cells, outside which is a layer of mesenchyme fairly richly supplied with capillaries and invested by a thin layer of mesothelium. Their inner surfaces are not smooth but are marked out irregularly into a number of quite shallow but wide depressions (fig. 31, *r.ch.p.*), delimited by inwardly projecting ridge-like thickenings of the wall or more rarely by low septal ingrowths (*spt.*). These depressions are the forerunners of the respiratory chambers of later stages, the "Luftkammern" of Selenka (*loc. cit.*, p. 159).

In addition, the lung-cavity is produced into a small number of diverticula, in the form of quite short cul-de-sacs (fig. 31, *div.*), the right lung terminating in three such diverticula and the left, in two, in series 5, 20.10.VII.02. They appear to be remnants of the diverticula of the lung cavity, seen in late uterine stages which have not yet expanded.

The conditions described above hold good for three specimens from three different litters but in two specimens from litter 28.VIII.98, there are some noteworthy differences. The lungs only partially fill the pleural cavities, having failed to expand fully. The right lung is distinctly lobulated, the left much less so. The pulmonary cavity is relatively small and is produced into well-marked diverticula, lined as is the rest of the cavity by a cubical epithelium which tends to thin out over the capillaries. Its mesenchymatous wall is very thick and richly vascularized. In these specimens, the embryonic condition of the lungs appears to have persisted longer than usual.

On the other hand, the structural condition of the lungs seen in specimens of litter 1.VII.05 and of stage B readily falls into line with that in the unattached young first described.

The pulmonary cavity is fully expanded, its walls are thin and contain capillaries, whilst its inner surface is very incompletely marked out into relatively large

respiratory chambers by irregularly spaced thin septal ingrowths, also carrying capillaries (Pl. 6, fig. 32, *r.ch.* and *spt.*). Sometimes these chambers are partially closed off by the fusion of the inner edges of the septal ingrowths. The importance of these latter lies in the fact that they increase considerably the surface-area available for the respiratory exchanges. Only a single diverticulum was observed at the posterior extremity of the right lung in one specimen of stage B.

The respiratory epithelium is composed of a single layer of cells varying in form from low cubical to flattened, but where it overlies a capillary, it is not infrequently reduced to a quite thin squamous layer containing small flattened nuclei. Bremer (1904) has described a similar thinning out of the epithelium over the capillaries in the new-born Opossum.

The lung in stage B recalls that of the latter as figured by Selenka (*loc. cit.*, fig. 4, Taf. XXIX) and by Bremer (1904, figs. 1-4), except that the septal ingrowths are much less numerous and the respiratory chambers consequently are much less regularly developed than they appear to be in the Opossum, judging from Bremer's fig. 3.

Figure 33 (Pl. 7) illustrates the condition of the lung as seen in longitudinal section in stage F. It shows the continuous lung-cavity and the large peripheral respiratory chambers (*r.ch.*), separated by the now well-marked septal ingrowths (*spt.*) which are rich in capillaries. The respiratory epithelium lining the chambers is reduced to a quite thin layer of cells, with minute nuclei.

Selenka (*loc. cit.*, p. 159) did not describe the lungs of the new-born Opossum in any detail but his figure of a section through the thorax shows the lungs as large expanded sacs, filling the pleural cavities and with their thin walls produced into septal ingrowths, irregularly spaced and of varying height and sometimes joined together by the fusion of their inner edges. The peripheral compartments so delimited he spoke of as "geräumiger Luftkammern" and apparently regarded them as precociously formed simple alveoli.

He pointed out that the lungs of the Opossum embryo must develop into functional organs during the last three days of intra-uterine life and that they have at their disposal neither the necessary structural material nor the time to develop a very large number of alveoli and so can only produce some dozen spacious air-chambers as a purely provisional breathing apparatus.

Bremer (1904) has also described the structure of the lungs in the new-born Opossum but in more detail than did Selenka. Whilst generally agreeing with the latter, he regarded the cavities of the lungs as "bronchi" and the respiratory chambers as "bronchioles", but clearly these terms, if justified at all at this stage, require qualification by the addition of prospective before each. He described and figured the respiratory epithelium, and showed that directly over the capillaries, its cells become thin and squamous, whereas in the intervals between them, they remain cuboidal.

He emphasized as did Selenka, the similarity of the lung of the new-born Opossum to that of the reptile (*Lacerta*) in the arrangement of the air-chambers opening into a "dilated main bronchus" and in the structure of the respiratory epithelium and concludes "that we find in the lung of the Opossum an epitome

of the evolution from reptilian to mammalian lung " (p. 73). But, as Selenka has pointed out, the lungs of the new-born marsupial exhibit a purely provisional structure, adapted to meet its particular circumstances and needs and we should hesitate to attach phylogenetic significance to this similarity.

(b) *Diaphragm.*

The diaphragm is established as a complete partition with a convex anterior surface, separating the thoracic and abdominal cavities. But it is not yet fully formed developmentally since its lateral marginal portions attaching it to the body-wall and formed by the pleuro-peritoneal membranes are still very thin and non-muscular, whilst the middle portion of its ventral marginal region, constituted by the pericardio-peritoneal septum, is also devoid of muscle fibres immediately above its attachment.

The remainder of the more ventral portion of the diaphragm, however, is well provided with transversely running fibres, whilst its dorsal portion is occupied on either side of the middle line by the longitudinally coursing fibres of paired muscle bundles which run forwards and downwards from the root of the dorsal mesentery, between the stomach on the left and the post-caval vein and the liver on the right side, to enter it. These bundles are remarkably strongly developed and would seem to represent the future dorsal pillars or crura of the diaphragm.

The diaphragm is still largely adherent to the liver but this, evidently, does not seriously interfere with its functional efficiency since the young one is able to breathe.

Selenka (*loc. cit.*, p. 158) records that in the new-born Opossum, the inspiratory rate is 24 to 26 per minute and the heart-beat about 60 per minute.

In how far the chest-wall, at this stage, is capable of participating in the respiratory movements, it is impossible to say, but the ribs are formed and reach the sternum and the intercostal and other muscles related to it are well developed.

ALIMENTARY CANAL.

Although the alimentary tract in the new-born young is complete as is to be expected since it has to be able to feed and to absorb the secretion of the mammary glands, it has no functional glands connected with it, its muscular coat is not yet developed, and its mucous membrane is represented only by the lining epithelium and the very thin undifferentiated vascular mesenchyme underlying it and forming the axes of the villous folds of the small intestine. These villous folds attain their maximum development in the duodenum and it is this section of the gut which is presumably the main absorptive region.

In this connection, it is worthy of note that, at the time of parturition, only a clear serous-like fluid can be expressed from the nipple* and that O'Donoghue (1911) in his study of the growth-changes in the mammary apparatus of *Dasyurus* records (p. 204) that in stages A and B, " no sign of milk is to be found either in

* This fact has already been recorded, in the case of the Opossum, by Dr. Barton in his letter of 1806 (see p. 353). He wrote (footnote to p. 351 of reprint): " But the milk that is afforded to the embryos, for a few days after their first reception into the marsupium, is nearly pellucid or transparent".

the alveoli or in the ducts, although there is a fair amount of a colostrum-like secretion present". He goes on to state that true milk first appears in stage C but is present only in the alveoli, whilst in stage C', about thirty-six hours after birth, it is also found in the main ducts.

In the unattached young of litter 20.10.VII.02 (series 5), the alimentary tract has the following disposition :—The stomach (Pl. 7, fig. 35, *st.*, from litter 1.VII.05) situated on the left side, appears in transverse section as a pear-shaped sac, 0.35 mm. in transverse diameter and 0.49 mm. in dorso-ventral diameter, down to its junction with the duodenum. It consists of a fundus region, a body into which the oesophagus (*oes.*) opens on its right side and a gradually narrowing pyloric region which opens through the pyloric constriction into the duodenum, the oesophageal and pyloric openings being 0.22 mm. apart. It is lined by a low columnar to cubical epithelium, measuring up to 0.012 mm. in thickness. Outside the epithelium, its wall is formed by a relatively thick layer of undifferentiated mesenchyme, covered by a mesothelial layer. Myoblasts are not yet recognizable. Its lumen, like that of the duodenum, contains a granular material in which there are present numerous finely granular spherules, together with considerable numbers of formed elements (foetal blood-corpuscles, leucocytes and very small spindle-shaped cells). This conglomerate represents extraneous material which the young one has sucked up, most of it probably during its passage to the exterior, through the median vagina, the pseudo-vaginal passage and the cloaca.

Behind the stomach and liver, the first limb of the duodenum (*dd.*) occupies practically the entire width of the abdominal cavity, measuring 0.71×0.43 mm. in diameter. It continues back on the right side (Pl. 7, fig. 36 (*dd.*)) and gradually becoming reduced in diameter, it finally undergoes a right-angled ventral flexure and passes into the ileum (fig. 35, *il.*) which runs forwards for a distance of 0.10 mm., immediately to the left of the duodenum and opens into the large intestine (fig. 36, *o.il.*). From the ileo-colic junction, the ileum continues forwards for 0.04 mm. and ends blindly. This very short cul-de-sac would seem to represent the caecum which is stated to be absent in the adult *Dasyurus* (Owen, 1841, p. 330; Huntington, 1903, p. 206, fig. 355; Hill & Rewell, 1954, p. 194). Behind the duodeno-ileal junction, the ileum is continued back to the right of the rectum as a second blindly ending diverticulum (0.06 mm. in length) of unknown significance.

The large intestine (fig. 36, *l.i.*) in comparison with the small intestine is of remarkably small diameter. It is disposed to the left of the duodenum and after making a small number of convolutions, continues back as the rectum to open into the rectal segment of the cloaca.

Apart from its large size and the thinness of its wall, the most striking feature of the duodenum are the prominent villous folds into which its lining is produced (figs. 35 & 36, *dd.*). Each fold consists of an axis formed by a capillary loop accompanied by a small amount of mesenchyme and the covering epithelium. In uterine stage ϵ , the capillaries in the folds are greatly enlarged, sinusoidal-like as Heuser (1921) states is also the case in the uterine embryo of *Didelphis* shortly before birth but in the new-born young, they are mostly collapsed and inconspicuous. (Pl. 8, fig. 37, *cp.*).

The epithelium deserves more detailed mention since it is the absorptive layer and exhibits interesting cytological changes with age. It is formed by a layer of columnar cells, with conversely projecting outer ends covered by a cuticular border and separated by distinct cell-membranes. In the unattached young, it has a thickness of about 0.017 mm. The nuclei are mostly oval, deeply staining and situated centrally. The cytoplasm basally and around the nucleus is dense and deeply staining but above the nucleus, in the distal portion of the cell-body, it stains lightly and is faintly granular.

In the recently attached young (1.VII.05), the epithelium is on the average, slightly thicker (0.017–0.021 mm.). The nuclei mostly quite large, are sub-central or basal and in the cytoplasm above the nucleus, there is present in many of the cells a lighter staining reticular area which in other cells is replaced by a definite vacuolar space, containing a light staining, faintly granular material.

In stage A (litter, 28.VIII.98) also recently attached, the epithelium is very similar to the foregoing. The cell-body above the nucleus is occupied by a finely granular reticulum but definite vacuolar spaces have not yet appeared (Pl. 8, fig. 37, *ep.*).

In both these recently attached young, there is now added to the extraneous material present in the stomach and duodenum of the unattached young, the mammary secretion, in the form of a dense finely granular coagulum, often vacuolated where it lies in contact with the epithelium (fig. 37, *m.s.*).

In stage B, the villous epithelium has altered considerably and is evidently now much more actively functional in the absorption of the mammary secretion. It has doubled in thickness compared with that of stage A, measuring 0.034–0.043 mm., and over extensive areas of the villous folds, its cells appear greatly vacuolated (Pl. 8, fig. 38, *ep.*). Their large and plump nuclei, mostly oval in form, usually lie near the mid-region of the cell-bodies, in contact with the cell-membrane but they may also be basal, especially in the cells lining the intervals between the villous folds. In the available sections, the cytoplasm is inconspicuous and appears to be located around the nucleus, whilst the major part of the cell-body is occupied by a large vacuolar space.

These spaces frequently appear empty but closer examination usually reveals the presence in them of a faintly staining substance.

In other cells, on the other hand, the vacuoles are more or less completely filled by a homogeneous material, usually only slightly eosinophil but not infrequently staining as deeply as the mammary secretion or even more deeply than that (Pl. 8, fig. 39, *cgl.*).

Heuser (1921) has given a detailed account of the anatomy and histology of the alimentary tract in the Opossum embryo shortly before birth and the pouch-young, three days old. So far as the anatomy of the tract is concerned, the general disposition of its parts is very similar in *Didelphis* and *Dasyurus*. In both, the duodenum is the widest region of the gut and in both, villous folds of its lining are markedly developed. Heuser found some of the cells of their covering epithelium in the pouch-young filled with a non-staining substance and others partially vacuolated but evidently in the stage he studied, vacuolization of the cell was not nearly so extensive as in our stage B. He left the question open as

to whether the inclusions he found in the epithelial cells were "products of secretion or of absorption" but there can be little doubt that the material in the cells of our stage B belongs to the latter category.

Glands.

The *submaxillary glands* are becoming slightly lobulated. Their ducts are still solid.

The *liver* is marked out by ventral fissures into three lobes, a central and right and left lobes, the right being the largest of the three. Its trabeculae are established.

The gall-bladder, situated in the middle lobe and the ductus choledochus are patent, the latter opening into the duodenum on its dorsal side, shortly behind the pylorus.

The dorsal pancreas is alone present and is slightly lobulated. Its duct reaches down close to the duodenum but in all the specimens examined it has lost its opening into it. Tribe (1918) records that out of thirty-three embryos and pouch-young of *Trichosurus* examined, the dorsal pancreatic duct persisted in seventeen and had degenerated in sixteen and that the duct may be present or absent in one and the same stage. Moreover, she states that so far as she is aware, "in no adult marsupial has the existence of a dorsal pancreatic duct been recorded" (p. 316).

VASCULAR SYSTEM.

Blood.

The red corpuscles are oval nucleated discs. In stage D, nucleated corpuscles still predominate in the blood but non-nucleated corpuscles are now present as well, the liver having begun to assume its haemopoietic function.

In stage F, though numbers of nucleated corpuscles are still left, the great majority of the corpuscles are non-nucleated and leucocytes have made their appearance in small numbers.

Heart.

The heart in its stage of development corresponds very approximately with that of the Rabbit embryo of G.L. 7.5 mm. (stage X of Girgis, 1930) and so far as can be judged, with that of the Opossum embryo of the last half of the eleventh day or the first half of the twelfth day (McCready, *loc. cit.*).

The ventricular region is disposed obliquely, its left margin being directed upwards to the left so that it lies adjacent to the pleuro-pericardial membrane and its right margin downwards and to the right so that it lies in contact with the ventro-lateral portion of the thoracic wall. The inter-ventricular septum is very incomplete and marks off the continuous ventricular cavity very unequally into a large left, and a smaller right division. Trabeculae are well developed, especially in the left ventricle.

The atrial division of the heart (Pl. 8, fig. 40; Pl. 9, fig. 41) situated cranially to the ventricle and directly above the bulbus cordis, appears as a very large thin-walled chamber, incompletely subdivided by the septum primum (*s.pr.*) into a large left (*l. atr.*), and a smaller right atrium (*r. atr.*). The crescentic septum

primum arising from its dorsal wall extends a little more than halfway through the atrial cavity so that the primary foramen ovale is very large (Pl. 9, fig. 41, *pr.fo.*). The septum is perforated by some four small secondary foramina, a large one (*pf.*) and a minute one shortly below its attachment and two smaller ones lower down. These foramina are all there are to represent the markedly fenestrated condition of the septum seen in certain other marsupials. This condition seems to have been described first by Beard (1897) in a uterine embryo of *Trichosurus* (G.L. 14 mm.) where he states "the foramen ovale is an open network" (p. 80). Later the same condition was described and figured by McCrady (*loc. cit.*) in the Opossum embryo from the second half of the 12th day (see his fig. 51, p. 157). At this time also, McCrady states (p. 156) that the septum primum has reached the endocardial cushions of the atrio-ventricular opening and that at birth it "still shows a few very small perforations" (p. 197) which gradually become over-grown so that a few days after birth the two atria are completely separated. In the new-born young of *Trichosurus* (G.L. 14.8 mm.) both Beard (*loc. cit.*) and Broom (1898) state that the foramen ovale is closed; presumably they refer to the secondary fenestrations. In stage B, the septum primum is in much the same condition as in stage A, the primary foramen ovale being still quite large, but it is not perforated, though there is a minute, very thin, pit-like area shortly below its dorsal attachment.

The septum secundum is absent as McCrady (p. 156) states is also the case in the Opossum.

As McCrady points out, the lack of the septum secundum and the fenestrated condition of the septum accounts for the absence of a fossa and annulus ovalis in the marsupial heart, first noted by Owen (1834) in the heart of the Kangaroo.

The septum spurium (Pl. 8, fig. 40, *s.sp.*) is present and is well developed. Cranially it delaminates off from the ventro-lateral corner of the right atrial wall and increasing in extent as it is traced back, it finally becomes continuous dorsally with the cranial margin of the sinu-atrial opening, whilst ventrally it joins the floor of the atrial cavity immediately to the right of the junction of the septum primum with the same. It thus subdivides the cranial portion of the right atrial cavity into lateral and medial portions. The atrio-ventricular canal is disposed obliquely so that its endocardial cushions lie not dorsally and ventrally but obliquely on its right and left sides and the blood-flow is directed into the right ventricle.

The sinus venosus is an extensive thin-walled chamber of very irregular form which consists of the two sinus horns, right and left, an obliquely disposed canal connecting the two, and a transversely wide caudal extension which runs back dorsally to the ventricular region of the heart for a distance of 0.072 mm. behind the caudal margin of the opening of the postcaval vein into the right horn.

The right sinus horn (figs. 40, 41, *rh.sv.*) which is larger than the left, cranially overlies the lateral portion of the right atrium and extends caudally to overlie the right ventricle. It opens into the right atrium by the slit-like sinu-atrial opening guarded by well-marked right and left venous valves (fig. 41, *rh.sv.*), the right valve being the more extensive of the two. The right precaval vein (fig. 40, *r.pv.*) opens directly into it shortly in front of the sinu-atrial opening and

some distance behind that, the postcaval vein opens on its dorsal wall (Pl. 6, fig. 30, *pcv.*). At the same level, the left sinus horn with which the left precaval vein is directly continuous, crosses the mid-line as an obliquely disposed canal which opens into the right horn dorso-laterally, (fig. 30, *lh.sv.*).

It is perhaps deserving of notice that, whilst the left precaval vein merges insensibly into the left sinus horn, the opening of the right precaval vein into the right sinus horn is clearly marked by a slight lateral infolding and consequent narrowing of the lumen, at the junction of the thin wall of the vein with the thicker lateral wall of the sinus horn (fig. 40).

The common pulmonary vein opens into the left atrium immediately to the left of the attachment of the septum primum. It runs back below the trachea and is formed by the union of the two pulmonary veins, one from each lung.

The bulbus cordis is noteworthy in that it possesses only two bulbar cushions instead of the usual four present in the bulbus of the Eutherian embryo. Coincidentally with the freeing of the bulbus from the right ventricle, dorsal cushion (A) appears on the right dorso-lateral side of the bulbus lumen, then 0.08 mm. in front, cushion (B) appears on the left ventro-lateral side of the lumen. Traced forwards, the cushions increase in size and moving anti-clockwise, come to occupy a lateral position facing each other, (A) on the right, (B) on the left. Then (A), the larger of the two, moves into a right ventro-lateral position, (B) becoming left dorso-lateral (Pl. 9, fig. 41, *ec.A*, *ec.B*). This spiral twisting proceeds through the full 180° so that (A) originally dorsal, becomes ventral and (B), dorsal (Pl. 8, fig. 40), and two lateral channels are left connected by a narrow chink between the two inwardly projecting cushions. Twisting continues through a further 20° or so, so that (A) comes to occupy the left ventro-lateral side of the bulbus and (B), the right dorso-lateral side. Fusion of the cushions finally takes place, leaving a right ventro-lateral channel and a left dorso-lateral. These channels then become ventral and dorsal in position and they finally separate as two distinct vessels, superimposed the one on the other, the larger ventral forming the aortic arch and the dorsal, the pulmonary artery. There is no ductus arteriosus.

The aortic arch after giving off in known fashion, the common stem for the common carotids and the left subclavian artery and on the right, the right subclavian artery, runs back as the dorsal aorta, to the left of the oesophagus and the trachea (Pl. 9, fig. 41, *d.a.*). The pulmonary artery passes up to the ventral side of the trachea and turns back below it, to reach the lungs.

VENOUS SYSTEM.

The development of the postcaval vein, the hepatic venous system and the allantoic vessels in a series of Australian marsupials (including *Dasyurus*) has been described in detail by Tribe (1923).

Our own observations, so far as they relate to the new-born *Dasyurus*, serve merely to confirm her results. In that stage, the post-renal section of the post-caval vein is not yet established, but its mesonephric or subcardinal, and its hepatic and prehepatic sections are in functional use and as Dr. Tribe has shown there is present as in *Perameles*, a renal-portal mesonephric circulation.

The following statements refer in particular to an unattached specimen of litter 20.VII.02, series 5, in which the mesonephroi have a total length of about 0.97 mm.

The posterior cardinal veins (Pl. 9, fig. 43, *r.pc.v.*, *l.pc.v.*) are relatively large vessels which extend forwards over the caudal portions of the mesonephroi and finally disappear over or just in front of the subcardinal anastomosis. About 0.20 mm. in front of the caudal extremities of the mesonephroi, the posterior cardinals extend down on the medial sides of the latter, as far as the dorsal attachment of the mesentery and from their ventral extremities there separate off the subcardinal veins (fig. 43, *r.sc.*, *l.sc.*). These continue forwards and shortly behind the mid-regions of the mesonephroi, unite to form the extensive subcardinal anastomosis, 0.09 mm. in length, which at its cranial extremity divides into a large right, and a much smaller left vessel. Immediately behind the anastomosis, the left posterior cardinal is in wide open communication with the left subcardinal (fig. 43, *l.pc.v.*, *l.sc.*).

At the level of the division of the subcardinal anastomosis, the right posterior cardinal has already disappeared, whilst the left continues forwards for a very short distance before it also fades out. The left subcardinal continues forwards for about 0.22 mm. before it also disappears.

The entire drainage of the mesonephroi thus devolves on the right subcardinal (fig. 42, *r.sc.*) which constitutes the efferent vessel of the mesonephric renal-portal system, the afferent vessels of which are the posterior cardinals. As shown by Dr. Tribe, the right subcardinal and the subcardinal anastomosis together form the subcardinal or mesonephric section of the postcaval vein.

The right subcardinal (fig. 42, *r.sc.*) runs forwards medially to the cortical suprarenal primordium (*csp.*) and shortly behind the cranial extremity of the mesonephros comes to lie below that primordium, superficially imbedded in a groove on the dorso-medial surface of the right lobe of the liver. Continuing its superficial course along the latter, it runs directly below the diaphragm and is joined, by way of the ductus venosus, by the omphalo-mesenteric, now actually the portal vein. The conjoint trunk so formed constitutes the hepatic section of the postcaval. It passes through the diaphragm and runs forwards attached to the right pleuro-pericardial membrane as the prehepatic section of the postcaval (Pl. 6, fig. 31, *pcv.*), to open on the dorsal side of the right sinus horn as noted above.

The two allantoic veins (now purely body-wall veins) unite to form a common trunk some distance in front of the umbilicus, which passing up by way of the ventral mesentery and the right lobe of the liver, directly enters the hepatic section of the postcaval just before it perforates the diaphragm.

UROGENITAL SYSTEM.

(Pl. 9, figs. 42, 43, 44.)

As is well known, the mesonephroi in the later uterine embryos and the new-born young of the marsupials reach a relatively large size and are functionally active excretory organs both before and for some little time after birth (Buchanan & Fraser, 1918 pp. 45-6, and for the experimental evidence, see Gersh, 1937).

Dasyurus is no exception. In the new-born young, the mesonephroi are two elongated slightly curved bodies which attain a length of up to 1.20 mm. and a maximum thickness of about 0.25 mm. They begin behind the dorsal attachment of the diaphragm to which they are connected by quite short mesenteric folds and extend back gradually decreasing in size to the pelvic region.

The mesonephros of *Dasyurus* appears to be unique in the marsupial series in that typical glomeruli are absent.

In a transverse section through its mid-region (Pl. 9, figs. 42, 43), the Wolffian duct (*w.d.*) is seen lying below its lateral or ventro-lateral margin, whilst its dorsal half is occupied by the secretory tubules (*s.t.*) and its ventral half or so, by elongated cavities (*gl.c.*) disposed horizontally or obliquely and separated by narrow septa (*gl.s.*) carrying capillaries and well seen in longitudinal or horizontal sections through the organ (Pl. 9, fig. 44). Into each of these cavities, a secretory tubule opens (figs. 42, 44, *s.t.o.*) and there can be no doubt but that they represent the glomerular cavities of the typical malpighian corpuscles. They are lined each by a thin layer of more or less flattened epithelial cells, quite distinct from the epithelium forming the walls of the secretory tubules. This latter epithelium is composed of cubical cells with centrally situated oval or flattened nuclei, the inner ends of the cells frequently projecting convexly into the lumen, whilst their cytoplasm, especially after Zenker fixation, is strongly eosinophil (fig. 44, *s.t.*). The collecting segments of the secretory tubules are narrower and open on the dorsal side of the Wolffian duct (fig. 43, *c.t.*). Unlike the sinusoidal capillaries between the convolutions of the secretory tubules which are richly developed and especially so in the late uterine embryo, the capillaries in the septa between the glomerular cavities are necessarily small and not at all conspicuous, nevertheless such as they are, they must be regarded as representing the glomeruli of normal malpighian corpuscles, but here each group of septal capillaries is common to two adjacent glomerular cavities.

The origin of this curious and aberrant condition remains to be investigated as well as the problem of the circulation of the blood in the septa.

The glomerular cavities and the lumina of the secretory tubules contain quantities of a finely granular material (fig. 44) and such is also found in the cloaca and in the allantoic canal.

The endodermal cloaca is approximately at the stage of development described by Buchanan & Fraser (*loc. cit.*) in their stage VIII of *Trichosurus* (G.L. 7.25 mm.), see their text-fig. 4, p. 54.

The allantoic canal passes back from the umbilicus, attached as usual to the ventral abdominal wall (there are no allantoic arteries accompanying it) and definitely enlarges to form the bladder primordium before it becomes continuous with the cranial extremity of the cloaca. At this level, the cloaca is distinguishable into an expanded dorsal portion into which the allantoic canal opens and which is lined by a thin layer of endoderm and a ventral portion which is laterally compressed and lined by a thicker layer of endoderm*. Behind, the allantoic opening,

* In a uterine embryo of Stage ζ, the cranial (endodermal) wall of the ventral segment is prolonged forwards, in contact with the ectoderm, as a solid median septum of gradually decreasing height, into the mesenchyme of what will be the genital tubercle. This septum we can only interpret as a most precociously formed urethral plate. We have not encountered it in any of the new-born young.

the Wolffian ducts open dorso-laterally into the dorsal segment by sagittally expanded orifices and very shortly behind these, the rectum opens dorso-medially into the laterally compressed caudal region of the cloaca. We can thus recognize its future urogenital and rectal segments though there is as yet no definite line of separation between the two.

The mesenchyme situated between the allantoic canal and the rectum and forming the urogenital septum is penetrated by a prolongation of the coelom for up to a little over two-thirds of its extent.

The cloacal membrane in one unattached specimen is still intact but its endodermal layer is degenerate over its caudal portion and its rupture appears to be imminent. In three other specimens, rupture in this region has taken place and the cloaca is open to the exterior.

The ureteric bud also closely resembles that of stage VIII, *Trichosurus*, of Buchanan & Fraser. It arises from the dorso-median, sometimes the dorsal side of the Wolffian duct shortly before it opens into the cloaca and consists of a narrow duct which ends in front in an expanded bulbous extremity, surrounded by a dense layer of nephrogenous mesenchyme (cf. Buchanan & Fraser, *loc. cit.*, p. 50). These authors state (p. 51) that in the pouch-young of *Dasyurus*, stage F, glomeruli are just beginning to develop in the permanent kidney, whilst in stage G, they are comparable with those of the pouch-young of *Trichosurus* of G.L. 17 mm. and H.L. of 7.5 mm. so that after birth the development of the permanent kidneys would appear to proceed fairly rapidly. They emphasize (p. 69) that the new-born *Dasyurus* "with respect to the cloacal region, as in all other points connected with urogenital system, is much less advanced than the corresponding stage of the *Trichosurus*".

The tail-gut has either completely disappeared or is represented by a solid remnant only. In uterine stage ζ (shortly before birth), it is short and luminated.

The gonadal primordia (genital ridges) are recognizable as slightly projecting thickenings, extending along the dorso-medial borders of the caudal portions of the mesonephroi, just below the attachment of the mesentery (Pl. 9, fig. 43, *g.r.*).

It is worthy of note that in the sections of unattached young and in one section in longitudinal series of stage B, the umbilical opening is still patent but doubtless, in life, the lips of the opening were in contact.

DUCTLESS GLANDS.

(a) *Thymus*.

In *Dasyurus*, the thoracic thymus is alone present, as in *Perameles* (Fraser, 1915), there being no trace of the superficial cervical thymus such as occurs in *Trichosurus* (Fraser & Hill, 1915) and other diprotodonts (Symington, 1898). In the Opossum, Kingsbury (1940) states that a variable and relatively slight thymic transformation of the cervical vesicle occurs but at a location neither superficial nor in the cervical position characteristic of the marsupials described by Fraser & Hill, and Fraser.

This observation does not appear to invalidate the conclusion of Symington (*loc. cit.*) that the Diprotodontia differ from the Polyprotodontia in the possession of the superficial cervical thymus.

Johnstone (1898) appears to be the only investigator who has examined the thymus in the adult, *D. viverrinus*. Owing to fatty infiltration, he found the thymus subdivided into some five lobular masses, two on the right, one on the left, and two smaller masses approximately median. He also examined the thymus in a pouch-young of *Dasyurus* sp. with a length of 7.5 mm. and found that it was "a paired body, consisting on either side of a smaller posterior and a larger anterior lobe". The latter measured approximately 0.4 mm. in greatest length and about 0.02 mm. in greatest width, whilst the posterior lobe had a length of about 0.10 mm. and a width of about the same as the anterior lobe. We have not encountered the conditions here described in any of our specimens. He found no trace of thymus in the neck, i.e. no superficial cervical thymus was present. In our comparable stage D, the thymus consists of two paired lobes, distinctly lobulated and situated immediately cranial to the pericardium. The right lobe measures 0.20 mm. in length and 0.15 mm. in dorso-ventral thickness, and the left, 0.22 mm. \times 0.18 mm. Immediately in front of the left lobe is an oval body, 0.060 mm. in length \times 0.043 mm. in thickness with an extremely minute lumen, round which the cells tend to be radially arranged. This may be epithelial body IV.

In stage F, the two lobes of stage D, have united across the middle line to form a bilobed lobulated mass, the lateral lobes of which have a cranio-caudal length of 0.31–0.32 mm. and a dorso-ventral thickness of 0.34 mm. In the lateral lobes, cortical and medullary zones are distinguishable and in the latter, Hassall's corpuscles are beginning to form.

In the new-born young, the thymus exhibits some variation in evident correlation with its degree of development.

In specimen B1 (20.10.VII.02), the thymus is composed on each side of two superimposed cellular cords, of which the ventral is the longer and thicker. On the right side, the ventral cord has a length of 0.08 mm. and the dorsal, a length of 0.048 mm. On the left, the ventral measures 0.10 mm. in length, and the dorsal 0.032 mm.

The right lobes are situated laterally to the stem of the common carotid arteries and the left, ventro-lateral to the same and both lie dorso-laterally to the anterior prolongation of the pericardial cavity.

Comparison with the thymus of *Trichosurus* (Fraser & Hill, *loc. cit.*) and that of the Opossum (Kingsbury, *loc. cit.*) suggests that the ventral thymus represents thymus IV and the dorsal, thymus III.

In series A, of the same litter, the thymus on the left side, consists of an elongated ventral cord 0.146 mm. in length \times 0.03 mm. in thickness and a superimposed dorsal cord, 0.094 \times 0.017 mm. On the right side, it consists of a single pyriform lobe, 0.14 mm. in length \times 0.038 mm. in thickness, its base resting on the wall of the anterior extremity of the pericardium.

In 1.VII.05 (long series), conditions are similar but reversed, the right thymus consisting of an irregularly lobulated ventral cord, 0.187 mm. \times 0.034 mm. and a

dorsal cord, 0.077 mm. \times 0.017 mm. The left thymus consists of a single lobule, triangular in outline in longitudinal section and 0.163 mm. in length \times 0.085 mm. in its maximum dorso-ventral thickness.

In three other specimens examined, the thymus consists of a single cord on each side, measuring up to 0.20 mm. in length \times 0.051 mm. in maximum thickness, but in one of them, the cranial half of the right thymus appears to be composed of two thin cords.

The evidence here presented would seem to indicate that paired thymus elements III and IV are present in *Dasyurus* as in *Trichosurus* and *Didelphis*, that thymus III is smaller than thymus IV and that they unite with each other to form a single cord on each side as sometimes happens in *Trichosurus* (Fraser & Hill) and in *Perameles* (Fraser) and that these cords after enlarging, unite across the middle line to form a single bilobed mass.

Epithelial Body IV is a small structure, usually situated behind, or dorso-laterally to the caudal extremity of the thymus but in one new-born it was found just cranial to the left thymus cord (cf. stage D, *ante*). It varies in size up to a maximum length of 0.072 mm. and a diameter of 0.038 mm. In three specimens it was not located with certainty.

Epithelial Body III occupies its usual position, dorsal to the common carotid artery, and just behind its point of division or its anterior extremity may lie dorso-medially to the internal carotid. It extends back below and behind the superior laryngeal nerve or may begin behind the latter. It appears as a more or less elongated, thin cellular cord, varying in length on the two sides, its maximum length being about 0.11 mm.

(b) *Thyroid gland.*

The thyroid consists of the usual two lateral lobes, variable in size, connected by an isthmus which may be thick when the lateral lobes are small or thin and discontinuous when the lateral lobes are well marked.

The *Ultimobranchial Bodies* (observed in only one specimen (stage A, *trans.*)) take the form of quite thin, flattened strands, which begin shortly behind the terminations of epithelial bodies III and extend back to the level of the cranial extremities of the lateral lobes of the thyroid but apparently fail to fuse with them. They reach a length of 0.09–0.10 mm.

(c) *Hypophysis cerebri.*

K. M. Parker (1917) has provided a detailed account of the development of the hypophysis in a number of Australian marsupials. In *Dasyurus*, only the earliest stages in its development are dealt with, but its structure in three pouch-young stages (H, I and J) is described in detail.

The earliest phase of its condition in the new-born young is seen in an unattached specimen of litter 20.10.VII.02, series 5.

The pars neuralis (the primordium of the posterior lobe) is represented by the elongated, slightly flattened infundibular process arising from the floor of the diencephalon and appearing laconic in longitudinal section (Pl. 11, figs. 49, 50, *i.pr.*).

As Miss Parker remarks, it appears relatively early in *Dasyurus*, being already present in conical form in uterine stage ϵ .

The pars buccalis (the primordium of the anterior lobe) is distinguishable into proximal (ventral) and distal (dorsal) lobes and has lost its connection with the hypophysial duct, a solid remnant of which may be present in the upper part of the hypophysial foramen. The latter may be patent, though quite narrow and occupied by a strand of embryonic connective tissue, or it may be completely closed.

The distal lobe (Pl. 10, fig. 48, *d.l.*) is transversely extended and possesses a wide lumen. Its dorsal wall, with which the infundibular process lies in contact, is thinner than its ventro-lateral walls. It measures about 0.15 mm. in length.

The proximal lobe (*p.l.*) underlies the distal and is in continuity with its ventral wall, being marked off from it by a circular constriction. It is much smaller and less wide than the distal, its length being about 0.07 mm. It possesses a narrow lumen which communicates with that of the distal lobe or the opening between the two may be closed and lumen restricted to its lateral halves (fig. 48, *p.l.*). At its cranial extremity, it terminates in a small median and two lateral lobules.

In slightly more advanced young, the dorsal wall of the distal lobe is indented by the infundibular process so that the lobe projects upwards dorso-laterally on either side of it, its lumen being crescentic. Otherwise, except for indications of lobule formation at its cranial and caudal ends, the distal lobe has not essentially altered. On the other hand, the proximal lobe has undergone a marked change. It has increased in extent so that its cranio-caudal length slightly exceeds that of the distal lobe and it has lost its lumen, except for a very slight penetration into it of the lumen of the dorsal lobe. Moreover, its lateral portions have proliferated to form irregular, more or less distinct small lobules, in which a minute lumen is sometimes detectable and between which slight mesenchymatous ingrowths have penetrated.

Altogether, the hypophysis of the new-born *Dasyurus* is very much less advanced developmentally than is that of the new-born *Trichosurus* as described by Miss Parker (*loc. cit.*, p. 207).

(d) *Cortical suprarenal primordia.* (Pl. 9, fig. 42, *csp.*)

These are paired, relatively massive, band-like formations which extend from close behind the anterior extremities of the mesonephroi back to the subcardinal anastomosis and the beginning of the gonadial ridges. They lie medially to the mesonephroi, reaching up from the coelomic epithelium with which they are in places still continuous, to the level of the dorsal aorta. They measure up to 0.17 mm. in height \times 0.11 mm. in breadth, and are composed of irregular cords of cells between which run capillaries.

SKELETON.

The future cartilaginous skeleton is at the stage of procartilage, the only exception being the ribs, which in later members of stage A, are assuming the condition of true cartilage.

*Chondrocranium.**

The chondrocranium of stage B has been modelled and figured though not described in any detail by Edgeworth (1935, figs. 683 and 683 *a*), that of a pouch-young of G.L. 8 mm. (=stage E) has been described and figured by Broom (1909, figs. 25 and 26, Pl. XVI (model) and figs. 27–32, Pl. XVII (sectional figures)), whilst Fawcett (1918) has provided a figure (Pl. XXI) of a model of that of a pouch-young of G.L. 9.3 mm. (=approximately stage G).

In the new-born young, the central stem (Fawcett, 1917) as seen in median longitudinal section, appears very shallow and saucer-shaped. Its caudal section formed by the parachordal (basal) plate slopes very gently downwards and forwards from the incipient atlanto-occipital joint, to its maximum curvature below the pontine flexure of the medulla, shortly behind the slight dorsum sellae and the very shallow sella turcica into which opens the hypophysial foramen, when patent. In front of the latter, the central stem now slightly thicker, is formed by the trabecular bar, which continues forwards and slightly upwards to become continuous with the nasal septum (Pl. 11, figs. 49, 50).

Polar cartilages not being detectable and taking the hypophysial foramen as marking the junction between the parachordal and trabecular regions of the central stem, the former is about three times the extent of the latter, in correlation no doubt with the greater development of the hind-brain as compared with the fore- and mid-brains.

It is also worthy of note that the chief constituent parts of the chondrocranium have already become joined up to form a continuous, though as yet very incomplete, case for the support of the brain and the olfactory organs, the olfactory capsules being the only parts which can be regarded as relatively well formed.

The chondrocranium of the new-born *Dasyurus* is at a much earlier stage of development than that of any marsupial hitherto described.

Olfactory capsules.

Transverse sections through the snout reveal the presence, shortly behind its anterior margin, of two plates of procartilage, which we may term the prenasal laminae (Pl. 3, figs. 18, 19, *pn.l.*). They occupy about the dorsal two-thirds of its interior and lie immediately above the ventrally situated group of sinusoidal capillaries (cf. p. 382). In B 3, they have each a width of 0.17 mm. and vertical height of 0.32 mm. Their medial margins are slightly convex and closely approximated, whilst ventrally they diverge downwards to terminate bluntly.

As the anterior margins of the external nares are approached, these laminae assume an x-shaped form, the ventral wings of the x curving outwards and downwards and being more extensive than the dorsal. Then between the external nares, the vertical limbs of the x fuse to form the nasal septum, whilst the lateral wings, dorsal and ventral, support respectively the dorsal and ventral rims of the narial openings.

* We are greatly indebted to Sir G. R. de Beer, F.R.S., for revising this section and providing interpretations of parts of the chondrocranium.

It would thus appear that, anterior to the narial openings, the nasal capsule is prolonged forwards on either side of the middle line as a very short semi-tubular extension closed in front by the expanded prenasal lamina which, with its fellow, serves for the support of the snout.

When traced back, the dorsal wings of the nasal septum are seen to increase in width, whilst the ventral wings gradually become reduced and seem either to fade out or to become continuous with two stout rods, disposed at first approximately transversely. These would seem to correspond to the anterior transverse laminae of authors. From their medial margins there separate off the very slender rod-shaped paraseptal cartilages (*vide* Pl. 4, fig. 23, *ps.c.* of stage D) which run back ventro-medially to Jacobson's organs and at this stage terminate behind them in free tips.

Immediately behind the posterior margins of the narial openings, the transverse laminae thicken and, extending up dorso-laterally to the outer sides of the nasal cavities, pass into continuity with downward extensions of the dorsal wings of the nasal septum, thus completing the lateral walls (*paries nasi*) of the nasal capsules. Their roof (the *tectum nasi*) is formed by the dorsal wings and, at the level of the olfactory bulbs, is perforated on each side by the epiphantal foramen, transmitting the ophthalmic ramus of the Vth nerve.

The nasal septum, very shortly behind the first appearance of the olfactory bulbs, loses connection with the *tectum nasi* and having meantime thickened, appears as a vertically elongated oval mass, whilst the postero-ventral moieties of the lateral capsular walls (representing the *cupolae posteriores* of the nasal capsule (G. R. de Beer)) have also thickened and just anterior to the openings of the olfactory sacs into the posterior narial passage, separate off as longitudinally running ventral bars situated laterally to that passage (cf. de Beer 1929, text-fig. 19, *cp.*).

The dorso-lateral portions of the capsular wall continue back laterally to the brain as continuous bands representing the spheno-ethmoidal commissures the orbital cartilages and the orbito-parietal commissures (G. R. de Beer). They appear as vertically disposed curved strips which reach down almost to the optic stalks but decrease in height as they pass back and finally become continuous with the auditory capsules.

Trabecular and parachordal sections of the central stem.

Below the olfactory bulbs, the vertically oval continuation of the nasal septum merges into a transversely oval rod, the trabecular bar, and this, 0.05 mm. behind, becomes continuous laterally with the above-mentioned longitudinal ventral bars. There is thus formed a broad plate underlying the cerebral hemispheres and overlying the posterior narial canal as well as bounding it dorso-laterally. It is formed medianly by the thick trabecular bar, connected by thinner lateral strips with the slightly ventrally projecting longitudinal bars. These latter, when traced back, gradually become reduced and disappear shortly in front of the optic stalks, leaving the trabecular bar as a transversely oval rod.

From the level of the openings of the optic stalks into the third ventricle back as far as the hypophysial foramen, the trabecular bar shows evidence of its paired origin. It has meantime increased in width and behind that foramen, its continuation appears as a very slightly curved transverse plate, nearly as wide as the narial canal it overlies. This we regard as the commencement of the parachordal (basal) plate.

Almost at once, the parachordal plate passes into continuity laterally with two wing-like ventrally recurved procartilages, situated laterally to the posterior narial canal and below the semilunar ganglia (Pl. 10, fig. 48, *pr.a.*). This cartilage is identified by Edgeworth (1935) as the processus alaris, in his figs. 687*b* of stage D and 689 of stage F. It probably also comprises the ala temporalis (G. R. de Beer). In series 5, 20.10.VIII.02, these wings extent back for a distance of 0.15 mm. before they disappear just behind the ventral openings of the carotid canals. In this series they are present in three sections on one side and in two on the other before uniting with the parachordal plate; in two other series (B3 and C3), they separate off from the latter and continue back as free oval rods for a maximum distance in B3 of 0.056 mm. These facts would seem to indicate that the wings arise independently of the parachordal plate.

The carotid canals run obliquely forwards and upwards through the parachordal plate, their dorsal openings lying ventro-laterally to the mid-region of the buccal hypophysis (Pl. 10, fig. 48, *c.c.*).

Caudally to the disappearance of the above-mentioned wings, the parachordal (basal) plate continues back as an at first thick, transversely disposed bar, concave below where it overlies the roof of the naso-pharyngeal canal (Pl. 12, fig. 56, *p.pl.*). Then between the apices of the cochlear pouches, it begins to become wider and thinner and behind the latter, assumes a very shallow, saucer-shaped form in section (Pl. 13, fig. 57, *p.pl.*) and this form becomes accentuated as it is followed back. The roots of the IX and X nerves emerge over its lateral margins, between them and the still mesenchymatous ventral portions of the auditory capsules and at this same level, is situated the most cranial of the three pairs of hypoglossal foramina, the remaining two pairs occurring at intervals more caudally, the last pair, 0.10 mm. in front of the incipient atlanto-occipital joint (for further details concerning the hypoglossal foramina *vide* p. 417).

Behind the auditory vesicles, the lateral margins of the basal plate are prolonged upwards, alongside the medulla, to form the vertically disposed occipital plates.

In series 5, 20.10.VII.02, the degenerate remains of the chorda are traceable forwards on the dorsal surface of the basal plate for a distance of 0.10 mm. but in other specimens, the chorda terminates above its posterior margin.

Auditory capsule.

The auditory capsule is as yet poorly developed. It is represented by a curved plate of procartilage which in front overlies the auditory vesicle and is continued down along the lateral aspect of the utricular region of the vesicle to just below the primordium of the horizontal semicircular canal (Pl. 13, fig. 57, *a.cap.*). It is also continued down for a short distance as a thin lamina along the medial side

of the primordium of the anterior semi-circular canal, in front of the endolymphatic duct. The remainder of the capsule, including its cochlear portion, is formed by condensed mesenchyme.

The capsule is continuous in front with the orbito-parietal commissure and it also appears to be connected behind with the occipital plate by a very slender short occipito-capsular commissure.

Membrane bones.

Ossifications representing the premaxillae, maxillae, palatines and dentaries are present. The premaxillae are massively developed in front for the support of the snout, though Broom (1909) states that in the 8 mm. pouch-young "the premaxilla is small and situated far behind the anterior part of the nasal cartilage" (p. 207).

Meckel's cartilages.

As appears to be normal for marsupial pouch-young, Broom (1909), Esdaile (1916), Meckel's cartilages are fused in front and form together a strong arc-shaped bar for the support of the lower lip. They are bowed outwards behind for the accommodation of the massive tongue and the nipple.

Auditory ossicles.

The auditory ossicles in the new-born *Dasyurus* are at a very much earlier stage of development than in the new-born *Didelphis* (McCrady, 1938) and in the recently born *Perameles* (Esdaile, *loc. cit.*).

The primordium of the malleus (Pl. 10, fig. 45, *mp.*) is constituted by the dorsal extremity of Meckel's cartilage and is distinguishable by its denser appearance, due to the fact that its cells are smaller, richer in cytoplasm and their limiting membranes much less obvious than in the rest of the cartilage. It exhibits a slight caudal prominence, all there is to represent the future manubrium.

Investing the convex upper surface of the malleus primordium is a dense meniscus-like layer of flattened mesenchyme cells, in which there is situated centrally a small nodule of procartilage, the primordium of the incus (fig. 45, *inc.*). It lies laterally to the vena capitis lateralis (external jugular vein) and the stem of the VIIth nerve and has a cranio-caudal diameter of 0.068 mm. and a thickness of 0.034 mm. The position of the incus, dorsal to the malleus, is a feature in which the marsupials agree with the monotremes and differ from the Eutheria (de Beer, 1937, p. 465).

The primordium of the stapes lies medially to the vena capitis lateralis and the VIIth nerve and dorso-caudally to the upper end of the tubo-tympanic recess (Pl. 10, fig. 46, *stp.*). On the right side (in L.S. 1.VII.05) it appears as a small rod-like mass of early procartilage, 0.06 mm. in transverse diameter and 0.086 mm. in thickness, which is pierced centrally by a strand of flattened mesenchyme cells but whether or not this represents a collapsed stapedia capillary could not be determined. Although less distinct, the same relations appear to hold good for the left stapes.

But in other specimens, it is penetrated for only a short distance by a capillary (distinctly so in uterine stage ϵ) or is imperforate. Fawcett (1916, p. 21) noted that in a pouch-young of *Dasyurus* (approximately of stage G) the stapes was not perforated by the stapedia artery and according to Doran (1876) in adult Dasyuridae it is columelliform without exception; but in view of the observations recorded above, it remains to be determined whether that condition is primary or secondary.

The stapes is situated about 0.10 mm. above the upper end of the procartilaginous segment of the cerato-hyal (fig. 46, *ch.c.*) and in uterine stage ϵ the stapes blastema is connected by a distinct tract of cells with the latter but in the new-born, there are only traces of this connection.

Hyoid.

The body of the hyoid (basi-hyal) is a short, transversely wide bar of procartilage, appearing vertically oval in sagittal section (Pl. 3, fig. 21, Pl. 4, fig. 22, *hy.c.*), which lies immediately behind and below the glosso-epiglottic sulcus at the base of the tongue and below the cranial half of the epiglottis. In T.S. stage A, it has a length of 0.11 mm. and a breadth of 0.28 mm.

Shortly behind its apex, it gives off on each side a short process which is continued dorso-laterally as a dense proligamentous strand of mesenchyme in which there is situated, at the level of the external auditory meatus, a short rod of procartilage about 0.09 mm. in length, representing the cerato-hyal (Pl. 10, fig. 46, *ch.c.*) the whole constituting the anterior cornu.

At its caudal extremity, the basi-hyal gives origin to two elongated, slender, rod-like posterior cornua which run back below the laryngo-pharyngeal grooves to terminate freely dorso-laterally to the origins of the thyroid cornua (Pl. 5, fig. 28, *pc.h.*).

Edgeworth (1935) has figured (fig. 695) a section through the "hyoid segment" in stage A, showing the body of the hyoid, the cerato-hyal cartilages and the related muscles.

Vertebral column.

The vertebral column is in an embryonic condition. It consists of a continuous rod of procartilage, with well-marked but still shallow inter-central constrictions and enclosing variable remains of the chorda. Paired neural arches are present which fail to meet above the spinal cord. The primordium of a hypo-centrum is also present, directly below the atlanto-occipital joint (cf. Pl. 4, fig. 22a, *hc.*).

Shoulder girdle.

The development and morphology of the shoulder girdle in uterine and pouch-young of various marsupials (including *Dasyurus*) has been dealt with at length by Broom (1897, 1899, 1902), whilst Watson (1918) in his paper on the evolution of the tetrapod girdle has described it in a uterine embryo (G.L. 11.5 mm.) of *Trichosurus*.

In the new-born *Dasyurus*, the scapula is a flattened rod-shaped cartilage, which increases somewhat in width dorsally and is produced into a caudally projecting process (cf. Broom (1902), fig. 1, Pl. 41 of a *Dasyurus* pouch-young of about stage D). From the middle of the ventral half of its cranial border, arises the acromion, in the form of a stout forwardly directed process, slightly bent ventralwards. This, at its cranial extremity, passes into a very slender strand, at first procartilaginous, which runs medially and ventrally and after a course of about 0.30 mm. joins the outer end of the clavicular primordium.

As Broom (1897) was the first to show, the coracoid in the young marsupial is well developed and reaches down to articulate with the sternum, as in the adult monotreme. It takes the form of a stout cartilage which is directly continuous with the lower end of the scapula and furnishes with that the glenoid cavity. It passes downwards, inwards and backwards to articulate with the presternum (cf. Broom, 1902, figs. 1, 2, Pl. 41).

Cranially to the presternum and between the descending coracoid processes, is situated the clavicular blastema, in the form of an arc-shaped band of condensed mesenchyme, presenting in favourable sections, a paired appearance (Pl. 10, fig. 47, *cl.b.*). In its outer ends, the clavicular ossifications are just appearing.

Closely applied to the ventral surface of the clavicular blastema is a second, also composed of condensed mesenchyme, which is thickened and projects down keel-like medianly and thins out on either side (fig. 47, *icl.b.*). It begins close behind the anterior extremity of the clavicular blastema, extends back below it and the manubrium sterni and thinning out, becomes continuous with the layer of mesenchyme, the future perichondrium, investing the sternum. Watson (*loc. cit.*) was the first to recognize this blastema and it is clearly shown in his fig. 25 of a transverse section of a uterine embryo of *Trichosurus* (G.L. 11.5 mm.). He labels it "omosternum" and suggests that it really represents the inter-clavicle, an interpretation with which we are in agreement. In another embryo of the same size, Watson states that it shows two points of ossification antero-laterally and no trace of cartilage. Broom (1902), on the other hand, records that in a pouch-young of *Dasyurus* of about stage H, a distinct omosternal cartilage is present on each side, situated between the pointed extremity of the sternum and clavicle (1902, fig. 5, Pl. 41). This cartilage is doubtless to be regarded as "secondary" cartilage.

Fore-limb.

The procartilaginous primordia of the limb bones are all present and well developed. In later specimens of stage A, the shoulder joint cavity is fully established but the elbow-joint is not yet formed and there are no joints between the phalanges.

Hind-limb.

The future hind-limb skeleton is represented by tracts of condensed mesenchyme. No muscle-primordia are recognizable.

Ribs.

The ribs are well formed and are becoming cartilaginous.

Dental lamina.

The first traces of the dental laminae are present in the anterior portions of the upper and lower jaws.

NERVOUS SYSTEM AND SENSE ORGANS.

The nervous system and sense organs in the new-born young exhibit a remarkable combination of embryonic and advanced features. The nervous system indeed, would seem to be at the lowest possible grade of structural differentiation compatible with a considerable degree of reflex activity, the new-born marsupial being an outstanding example of a purely reflex animal.

The fore-brain, apart from the olfactory bulbs, is largely in an embryonic condition. The cerebral hemispheres are simple vesicles, entirely devoid of a pallial layer and exhibiting only slight basal thickenings, forming the primordia of the corpora striata, whilst there are similar thalamic thickenings of the floor of the diencephalon, otherwise its walls are undifferentiated. The olfactory bulbs, however, are relatively well developed and much in advance of the rest of the fore-brain and bundles of olfactory nerve-fibrillae pass into them.

The floor of the mid-brain also exhibits some degree of differentiation but it is in the medulla oblongata and to a lesser extent, in the cerebellum and the cervical and thoracic regions of the spinal cord that differentiation reaches its highest level, as is to be expected in view of the co-ordinated reflex movements associated with crawling which the new-born young is capable of carrying out and which have been described in detail by Hartman (1920) and McCrady (1938) in the case of the new-born Opossum.

The optic and auditory organs are in an embryonic condition but the olfactory organs, provided as they are with olfactory sense cells, appear capable of functioning and such evidence as there is suggests the probability of the occurrence of free nerve-endings below the epidermis of the oral shield which may serve for the reception of of tactile stimuli.

The cranial nerves (with the exception of the eye-muscle nerves) and the cervical and thoracic spinal nerves and their related ganglia are all well established.

(a) Brain.

Median sagittal sections through the brain (Pl. 11, figs. 49, 50) show the marked primary (mesencephalic) flexure, the wide and deep pontine flexure and the slight cervical flexure overlying the incipient atlanto-occipital joint, also the extensive IIIrd ventricle (*ven.* 3) communicating by way of the narrow iter (*it.*) with the still more extensive IVth ventricle of the rhombencephalon (*ven.* 4).

The IIIrd ventricle is bounded in front by the thick lamina terminalis (*l.t.*) which slopes upwards and forwards from a depression in the floor, which is subdivided by a slight projection of the noticeably small chiasma-bed, into a small cranial pre-optic recess (*pr.r.*) and a slightly larger post-optic recess (*pt.r.*). At its upper

end, the lamina terminalis decreases in thickness and becomes continuous with the much thinner and quite narrow strip of the cranial wall of the ventricular cavity which forms the medial boundaries of the foramina of Monro and which slopes upwards and backwards to pass into the thicker diencephalic roof (*d.rf.*). The velum transversum is not distinguishable.

The caudo-ventral wall of the diencephalon is produced into the prominent infundibular process (*i.pr.*), overlying the buccal hypophysis (*hyp.*). As in other marsupials (K. M. Parker, 1917) it appears characteristically cone-shaped in longitudinal section.

From the infundibular process, the caudal wall of the diencephalon ascends almost vertically. It is indented above by a localized depression, the mammillary recess (*m.r.*), and shortly above that terminates in a rounded prominence, the posterior tubercle (*p.t.*), marking the junction ventrally of the diencephalon with the mesencephalon. The dorsal junction of these two regions is not accurately determinable since the posterior commissure is not yet formed and the diencephalic roof (*d.rf.*) passes without break into that of the mesencephalon. Whilst the roof of the latter (*m.rf.*) is relatively extensive, its floor is extremely short, extending only from the tuberculum posterius back to the rounded prominence (*p.rm.*) (the plica rhombo-mesencephalica), marking its junction with the floor-plate (*f.pl.*) of the rhombencephalon (Kingsbury, 1920). There is no fovea isthmi.

In the median section, the following parts are to be seen in the hind-brain: the extensive IVth ventricle (*ven.* 4), the median cerebellar primordium (*cb.m.*) in the form of a short concavo-convex thickening, continuous in front with the mesencephalic roof and behind with the tela chorioidea (*t.ch.*) which is already established and the floor-plate of the medulla oblongata.

Prosencephalon.

The cerebral hemispheres (Pl. 11, fig. 51, *c.h.*) above the level of the foramina of Monro appear in horizontal sections through the head as two transversely oval vesicles, approximated in the middle line and disposed obliquely in front of the diencephalon (*dien.*).

They communicate below by wide foramina of Monro with the telencephalic portion of the IIIrd ventricle (Pl. 11, fig. 52; Pl. 12, fig. 53), the foramina being bounded in front by the narrow median strip of the telencephalic wall and behind by two inwardly projecting folds of the lateral walls, the plicae telo-diencephalica (*pl.td.*), marking the line of separation of the telencephalic and diencephalic portions of the IIIrd ventricle.

The rostral surfaces of the hemispheres are capped by the olfactory bulbs well seen in figs. 52, 53, (*o.b.*), as well marked, forwardly projecting thickenings of their walls. The bulb (Pl. 12, fig. 55) consists of a cytoplasmic fibrillar basis in continuity with the ependymal layer of the wall, in which are situated relatively large spherical or oval nuclei, each with a single nucleolus but in the material available, it has not been possible to recognize discrete cell-bodies around them. The bulbs represent localized thickenings of the marginal and mantle layers and are connected below by marginal-mantle tracts with the primordia of the corpora striata. They

receive small bundles of olfactory nerve-fibrillae but we have been unable to trace these into connection with the olfactory sensory cells in the olfactory epithelium. Apart from the olfactory bulbs and their connecting tracts, the walls of the hemispheres are undifferentiated.

Figure 54 pictures a section passing through the now greatly reduced ventral portions of the hemispheres, in which the remains of the lateral ventricles are seen to be bounded behind by thickened inbulgings (*c.str.*) of the antero-lateral walls (that on the left side being at a slightly lower level than that on the right and so more prominent). These thickenings we interpret as the primordia of the corpora striata. They are formed by localized thickenings of the marginal and mantle layers, like the olfactory bulbs with which they are connected by tracts of similar constitution and they are also connected by like tracts with the thalamic thickenings mentioned below.

The diencephalon (fig. 51, *dien.*), transversely extended and roughly quadrangular in form in horizontal section, is specially characterized by the presence on its caudal (morphologically ventral) wall of two elongated (thalamic) thickenings, one on either side of the middle line which project more or less prominently into the ventricular cavity (figs. 52–54, *th.t.*).

They extend upwards into continuity with the ventro-lateral thickenings of the floor of the mid-brain (fig. 51, *th.t.*). Apart from the connecting tracts between the primordia of the corpora striata and the thalamic thickenings, the lateral and dorsal walls of the diencephalon are only just beginning to differentiate into their constituent layers.

Mesencephalon.

The mid-brain is transversely wide and encloses a correspondingly wide iter. Its roof, of uniform thickness, possesses a thin marginal layer and the cells of the mantle layer are just beginning to appear. Its floor, in marked contrast, shows two strongly developed ventro-lateral thickenings with distinct marginal and mantle layers, which connect the thalamic thickenings with the medulla oblongata (fig. 51).

Rhombencephalon.

The hind-brain forms the largest and most advanced region of the brain. The cerebellum consists of two parts, respectively median and lateral. The median part (Pl. 11, figs. 49, 50, *cb.m.*) takes the form of a flat or more or less curved dorsal plate, which anteriorly is marked out into lateral halves by a slight median groove, on either side of which is a slight ridge-like thickening formed by a localized differentiation of the wall into marginal and mantle layers (Pl. 12, fig. 56, *cb.m.*). The dorsal plate is continuous in front with the roof of the mid-brain and behind with the tela choroidea of the IVth ventricle. Laterally, its margins bend round ventrally and pass into lateral thickenings which are continuous with the anterior extremity of the medulla, in the region of the plica rhombo-mesencephalica (Pl. 3, fig. 18, *cbl.*). These thickenings of the lateral walls would seem to correspond to those regarded by Larsell (1935–36) as forming the anlage of the “corpus cerebelli” in the Opossum.

With the extension of the IVth ventricle laterally to form lateral recesses the lateral cerebellar thickenings are continued back as two obliquely horizontal laminae (Pl. 12, fig. 56 ; Pl. 13, fig. 57, *cb.l.*), in continuity above with the margins of the dorsal roof-plate and also as two thin vertical strips which form the lateral walls of the ventricular recesses and which are in continuity above with the lateral margins of the horizontal laminae and below, with the margins of the medulla. These vertical strips soon become reduced to form on each side a lateral tela choroidea (figs. 56, 57, *l.tc.*).

Behind the lateral recesses, the dorsal roof-plate and the lateral laminae gradually become reduced and with the lateral telae merge into the dorsal tela choroidea.

It is deserving of note that in the lateral cerebellar thickenings and their caudal continuations, the horizontal laminae, the marginal and mantle layers of wall are well developed.

Medulla oblongata.

The medulla (Pl. 12, figs. 53, 54, 56 ; Pl. 13, fig. 57) is, histologically, the most highly differentiated portion of the brain as well as by far the largest. A deep median sulcus, of variable width, floored by the floor-plate and a thin continuation of the marginal layer, divides the medulla into two lateral halves which at first are disposed horizontally but gradually assume an obliquely vertical disposition as they are followed back. A ventral evagination of the medullary margin on each side, extending forwards from the level of the endolymphatic duct for a very short distance, would appear to represent the rhombic lip (fig. 57, *rh.l.*).

The medulla on either side of the median sulcus is greatly thickened, all three of its constituent layers, ependymal, mantle and marginal being well developed but it is the mantle layer which forms by far the greater part of its thickness. There is no sulcus limitans either in the medulla or the spinal cord to mark the separation into basal and alar laminae. Nevertheless the mantle layer is fairly clearly distinguishable by the grouping of the neuroblastic nuclei present in it, into a much thicker, ventral paramedian (motor) zone (*m.z.*) in the basal lamina and a thinner, more diffuse dorso-lateral (sensory) zone (*s.z.*) in the alar lamina (figs. 54, 56, 57).

(b) *Spinal cord.*

The central canal (Pl. 13, fig. 58, *c.c.*) still retains its embryonic dimensions and relations, being closed above by the thin roof-plate and below by the floor-plate, though the marginal zone now extends continuously across the middle line below it. Both together form the roof of the widely open ventral groove (the future ventral fissure), which has resulted from the marked growth of the cord ventrally on either side of the middle line.

The cord is invested, except over the roof-plate, by the marginal layer which is locally thickened on either side of the dorsal portion of the central canal to form the dorsal funiculi (*d.f.*).

Its lateral walls are greatly thickened, attaining their maximum level with, and below the ventral portion of the central canal. As in the medulla, it is the mantle layer which forms by far the greater portion of that thickness. In the absence of a sulcus limitans, there is no clear distinction into basal and alar laminae but in the mantle layer, we can distinguish a much thicker and more extensive (motor) zone (*m.z.*) in the region of the basal lamina which extends up to about the level of the mid-region of the central canal and projects down ventro-laterally as the primordium of the anterior horn, well below the level of the floor of the central canal and a much thinner and very much less extensive sensory zone (*s.z.*) in the region of the alar lamina which tapers upwards to terminate below the ventral half of the dorsal funiculus.

With the exception of the first, the spinal ganglia (*sp.g.*) of the cervical and thoracic regions are well formed and large. They are dorso-ventrally elongated and narrow and extend from the ventral margins of the dorsal funiculi to below the ventral surface of the cord.

The first spinal ganglion (absent according to McCrady (*loc. cit.*, p. 133) in the Opossum) is present, being situated at the level of the interspace between the occipital arch and the arch of the atlas but is very variable in size. It may be so small as to be vestigial or it may reach a diameter of up to 0.10×0.085 mm. (in L.S. B 3.).

On the left side in L.S. 1.VII.05, an exceptional condition is present. Here an elongated club-shaped ganglionic strand begins just cranial to the neural arch of the axis and extends forwards, gradually tapering, to terminate at the level of the atlanto-occipital joint. The strand has a length of 0.40 mm. and a thickness at its caudal end of 0.068 mm. and of 0.018 mm. at its cranial end. Its thick caudal portion represents the second spinal ganglion, whilst its thin cranial extremity is the vestigial representative of the first spinal ganglion. On the right side, the first spinal ganglion is normal but quite small, measuring in length 0.068 mm. and in thickness, 0.051 mm., the corresponding measurements of the second spinal ganglion being 0.153×0.076 mm.

On the left side, in this same series, the third and fourth spinal ganglia are connected by a quite thick anastomosis.

On the left side of L.S. stage A, also, the second spinal ganglion is connected by a thin anastomotic strand with the vestigial first spinal ganglion.

The dorsal and ventral roots (fig. 58, *v.r.*) and the spinal nerve trunks (*sp.n.*) are fully established and the brachial plexus is formed. The sympathetic trunks are distinct in the cervical region and in the anterior portion of the thoracic region but behind that are difficult to detect.

(c) Cranial nerves.

The nerves consist of non-myelinated fibrillae, accompanied by sheath cells as Langworthy (1928, p. 238) has recorded for those of the pouch-young Opossum.

The eye-muscle nerves (III, IV and VI) and the optic and auditory nerves are not yet developed, in correlation with the embryonic condition of the optic and

auditory vesicles and the lowly state of organization of the brain. The remaining cranial nerves are normally constituted but exhibit some interesting features deserving of brief notice.

Trigeminal nerve.

The semilunar ganglion (Pl. 10, fig. 48, *gn.sl.*) is much the largest of the cranial ganglia, its sensory and motor roots are established and its constituent nerve cells (neuroblasts) appear to be well differentiated, possessing large cell bodies and oval or spherical nucleolated nuclei.

The ophthalmic nerve is slender and traceable forwards dorsally to the optic stalk. It continues upwards, passes through the foramen epiphaniale in the tectum nasi and so reaches the mesenchyme below the antero-dorsal portion of the oral shield.

The maxillary nerve is unexpectedly large. It passes forwards, gives off a palatine branch and spreads out fan-wise in the snout region, its fine fibrillar branches being traceable into the mesenchyme underlying the epidermis of the oral shield.

The mandibular nerve, still larger, passes downwards and forwards into the lower jaw, lying immediately above Meckel's cartilage. Terminal twigs of the nerve can be traced into the mesenchyme underlying the lower lip segment of the oral shield.

Exteroceptive nerve endings have hitherto not been described in the new-born marsupial but the distribution of the terminal branches of the trigeminal nerves just described suggests that they terminate in free nerve endings immediately below the epidermis of the oral shield, capable of being affected by external stimuli, tactile and thermal. In this connection, it is of interest to find that Langworthy (*loc. cit.*, p. 230) states that in the new-born Opossum, thermal stimuli seem to be effective when applied to the region of the face—the trigeminal area, whilst, with reference to the pouch-young, seven days old, he records (p. 208) that "cutaneous sensation appeared to be well developed so that the animal responded to heat, cold and touch over the whole body but particularly in the trigeminal region".

Facial nerve.

The geniculate ganglion lies in contact with the caudal border of the semilunar ganglion and cranio-laterally to, and in intimate contact with the auditory ganglion, from which it is quite distinct. Histologically it is similar to the semilunar and much in advance of the auditory ganglion.

From the ganglion, the facial (hyomandibular) nerve (Pl. 10, fig. 46, *f.n.*) passes downwards and backwards immediately to the lateral side of the stapes, then curves round ventrally behind the upper ends of the tubo-tympanic recess and Meckel's cartilage and continues down as a very slender curved nerve which terminates in the condensed mesenchyme behind the latter. Shortly below the upper end of Meckel's cartilage (the malleus primordium), the trunk of the nerve gives off, almost at a right angle, a short, stout branch which runs forwards and appears to terminate in the mesenchyme behind that cartilage (Pl. 10, fig. 45, *f.n.*). This branch probably represents the chorda tympani, which according to Goodrich (1915) is already present in the 5 mm. embryo of *T. vulpecula* (*vide* his fig. 5, Pl. 11).

Glossopharyngeal nerve.

The ganglion superius is small but distinct and is situated on the sensory root close below its origin from the dorso-lateral surface of the medulla. The stem of the nerve passes down immediately in front of that of X and emerges with the latter over the margin of the basal plate to reach the ganglion petrosum (Pl. 6, fig. 29, *gn.p.*) which lies dorso-cranially to the ganglion nodosum. The two ganglia may be separate, or they may lie in contact when there is a cellular connection between the two or they may be joined by a short anastomotic strand. The IX nerve (ramus lingualis IX) runs down laterally to the pharynx and is traceable into the base of the tongue. In one specimen only (L.S. 1.VII.05) structures which appear to be taste-buds to the number of two or three were detected on the posterior part of the tongue.

Vagus nerve.

The ganglion jugulare in the new-born young is difficult to locate precisely and seems to be situated on the stem of the nerve, shortly before it emerges over the margin of the basal plate and below the level of the ganglion superius. In later stages, it is located in the foramen jugulare.

The nerve arises from the medulla by several main rootlets (at least three or four). The more cranial rootlets converge downwards and are joined at the level of the upper margin of the basal plate, by the most caudal rootlet which is separated by a gap from the cranial rootlets and runs downwards and slightly forwards. This caudal rootlet would seem to represent the vago-accessorius component of the nerve. It is joined by the spinal accessory nerve just before the combined rootlets forming the stem or trunk of the nerve emerge over the margin of the basal plate, between that and the blastema of the ventral wall of the auditory capsule, the gap marking the site of the future foramen jugulare.

The stem of the nerve passes downwards and slightly backwards to enter the ganglion nodosum. It is formed proximally of two fascicles, the cranial representing the combined cranial rootlets and the caudal, the conjoined vago-accessorius and the spinal accessory nerve. Distally the two fascicles come together and spreading out fanwise, join the ganglion nodosum.

The ganglion nodosum is the second largest of the cranial ganglia and its nerve-cells like those of the semilunar ganglion appear to be well differentiated. They possess well-defined cell-bodies and their nuclei, mostly spherical, possess each a single centrally situated nucleolus. The ramus visceralis X is a large trunk which runs back through the neck, ventrally to the trachea, curves round below the arch of the aorta and continues back above the thin wall of the anterior extension of the pericardium. It has not been possible to trace it more caudally. The superior laryngeal nerve passes directly from the medio-ventral side of the nodosal ganglion to the laryngeal region.

Spinal accessory nerve.

The spinal accessory which is about the same thickness as the vago-accessorius, arises from the medulla as far back at least, as the second spinal ganglion. It passes forwards medially to the first spinal ganglion, at first close to the surface

of the medulla, then curves down to the medial side of the occipital arch and joins the vago-accessorius just before the latter emerges over the margin of the basal plate, with the stem of X, as noted above. It leaves the stem of X shortly above its junction with the ganglion nodosum and curving back is distributed to the sterno-mastoid muscle and presumably also to the trapezius muscle.

Hypoglossal nerve.

It is stated that the marsupials are distinguished from the eutherian mammals by the possession of "usually two pairs of hypoglossal foramina" (de Beer, 1937, p. 384). Esdaile (1916) found two pairs in *Perameles* and Broom (1909) the same number in *Trichosurus* and *Dasyurus*. Edgeworth (1935), however, shows three foramina on the left side of his fig. 683 of a model of the chondrocranium of *Dasyurus* stage B and in four out of six specimens examined, we find three pairs of foramina present, with corresponding rootlets emerging through them. In the two other specimens, there are only two pairs of foramina, a reduction probably due in one of them at least to the confluence on one side of the two caudal foramina originally present, and on the other of the two cranial foramina.

The three rootlets on each side converge downwards and unite close to the nodosal ganglion to form the trunk of the nerve which either runs through the caudo-lateral extremity, or round the caudal border of that ganglion. It then passes laterally to the ramus visceralis X and turning forwards as a relatively thick nerve, enters the base of the tongue and branches to supply the tongue muscles.

Froriep's ganglion (ganglion hypoglossi, Froriep (1822)).

Froriep's ganglion is either vestigial or absent. In L.S. 1.VII.05, it is represented on the right side by a minute group of cells (0.05×0.018 mm. in diameter) situated shortly in front of the plane of the atlanto-occipital joint and in line with and 0.10 mm. in front of the small first spinal ganglion. On the left side, as also on both sides in L.S. stage A, no trace of the ganglion was observed. McCrady (*loc. cit.*, p. 133) states that it is present in his stage 30 of the Opossum (eleventh-day embryo).

(d) *Sense organs.*

Olfactory organs.

The olfactory organs are of particular interest as being the only sense organs in the new-born young which appear capable of functioning since receptive cells, olfactory sense cells, are present in the olfactory portion of the nasal epithelium and olfactory nerve fibrillae can be seen to enter the olfactory bulbs, though in the absence of silver preparations, we have been unable to trace these fibrillae into connection with the olfactory sense cells. Selenka (*loc. cit.*, pp. 158, 159) considered that the new-born young of *Didelphis* probably possessed the sense of smell, in addition to what he termed the "Wärmesinn" whilst McCrady (*loc. cit.*, p. 193) states that "the olfactory organs . . . may possibly be in a functional condition" in view of the facts that "the olfactory epithelium is ciliated (*italics ours*) and nerve fibres from this epithelium enter the olfactory lobe in large numbers". Neither of these investigators make mention of olfactory sense cells.

In their anatomy, the olfactory organs in the new-born young conform to the normal mammalian type. The laterally situated external nares lead back into the nasal cavities which are relatively extensive, only narrowing below at the level of the lower portion of the nasal septum. There are as yet no turbinal ingrowths. The naso-palatine canals are fully developed. Each opens on the roof of the buccal cavity by way of a well-marked groove which begins 0.03 mm. behind the tip of the snout and extends back for a distance of 0.07 mm. before the naso-palatine canal opens into it. From its anterior opening the canal runs back for 0.08 mm. and opens on the floor of the nasal cavity, directly below the primordium of Jacobson's organ. This occupies its usual position on the medial wall of the nasal cavity, dorso-laterally to the paraseptal cartilage. It has the form in front of a thick-walled groove which closes off behind to form a short tube, its total length being about 0.06 mm.

Shortly behind the level of the anterior margins of the olfactory bulbs, the nasal cavities become reduced to their ventral moieties and take the form of two canals, roughly triangular in section, with their apices directed medially and situated ventro-laterally to the trabecular cartilage. Extending medially below the latter, the two canals unite to open into the transversely wide posterior narial passage.

The hard palate flooring the latter, shows distinct traces of a median septum representing the line of fusion of the palatal folds and in it are situated anteriorly, the laterally situated maxillary ossifications and posteriorly, the palatine ossifications.

Traced back, the narial passage becomes crescentic, the hard palate becoming thickened over its mid-region so that it projects into it as a prominent convex ridge (Pl. 10, fig. 48, *r.pl.*) which continues back along the velum palati or soft palate. Finally it passes into the naso-pharynx floored by the latter and characterized by the presence on each side of a dorso-laterally directed groove, the tubo-tympanic groove. These grooves lead back into the tubo-tympanic recesses which open into the pharynx immediately behind the posterior margin of the soft palate. The ventral lips of the openings are formed by the continuations of the lateral attached margins of the soft palate and these, becoming bent ventrally, form the commencement of the palato-pharyngeal folds.

As longitudinal sections show, the soft palate does not simply thin out as its posterior margin is approached, to terminate in a thin lip; on the contrary it undergoes a marked dorso-ventral expansion, so that its margin is by no means a thin edge but a relatively extensive surface, not quite flat but showing a slight depression below its upper border, towards which the forwardly bent tip of the epiglottis is directed. In the longitudinal sections of specimen A (still unattached), for example, the soft palate, 0.17 mm. in front of its free margin has a thickness of 0.086 mm., whereas at that margin it has a thickness of 0.17 mm., i.e. it is just twice as thick. This increase is largely due to the fact that it is produced downwards, in front of the epiglottis, as a well-marked laminar process (beak-like in the longitudinal sections of A) which projects into the transverse groove between the base of the tongue and the root of the epiglottis (the glosso-epiglottic sulcus).

The nasal epithelium.

The epithelial lining of the olfactory sacs is already distinguishable into olfactory and respiratory portions. The olfactory epithelium is by far the more extensive of the two. It forms the lining at the back of the external narial opening (and so is directly exposed to the air) and immediately behind that, clothes the roof and upper part of the medial wall and more posteriorly still, the upper part of the lateral wall as well.

The respiratory epithelium is limited to the narrow lower part of the cavity and to the lateral wall immediately behind the external naris. It is much thinner than the olfactory epithelium and so is readily distinguishable from it.

The olfactory epithelium (Pl. 13, fig. 59) reaches a thickness of 0.047 mm. and is composed of receptive cells, the olfactory cells and supporting cells, the latter the more numerous of the two. On its surface is a thin cuticular membrane, with terminal bars marking the limits of the outer ends of the supporting cells. These are elongated and possess correspondingly elongated oval nuclei (*n.sc.*) which stain less deeply than those of the olfactory cells.

The olfactory cells (*olf.c.*) possess pear-shaped bodies, the cytoplasm of which, above the nucleus, stains deeply and tapers upwards to the surface where it passes through the cuticular membrane and projects as a short spike-like receptive process, measuring up to about 0.0086 mm. in length (*r.pr.*). Their nuclei are mostly oval, not so elongated as those of the supporting cells and staining more deeply. The cells are distributed very irregularly between the supporting cells and often occur singly shortly below the cuticular border, but they may also lie more deeply and occasionally occur in small groups lying near the mid-region of the epithelium.

No very definite zonal arrangement of the nuclei of the constituent cells of the epithelium is recognizable though such seems to be present in the epithelium in uterine stage ϵ where the supporting cell nuclei are mostly superficial, whilst the olfactory cell nuclei lie near its mid-region and are spherical in form. The epithelium is limited below by an extremely thin basement membrane. Basal cells are not recognizable. There are no Bowman's glands connected either with the olfactory or the respiratory epithelium.

The respiratory epithelium varies in thickness from 0.017–0.023 mm. It is composed of columnar cells with close-set nuclei, sometimes distinguishable into superficial and deep, and in the material available is not ciliated.

The epithelium of Jacobson's organs is composed of columnar cells and is notably thick, reaching up to 0.043 mm.

Lastly, there remains to be mentioned the occurrence of curious clear, bleb-like structures, varying in form from more or less columnar to club-shaped and attaining a height of up to 0.012 mm. which project from the cuticular membrane of the olfactory epithelium opposite the outer ends of the supporting cells. They are bounded each by a thin limiting membrane inside which are traces of a hardly staining material. Whether these structures are artefacts or normal formations we find difficult to determine. If the latter, it may be suggested that they are products of the supporting cells which serve to prevent the drying of the surfaces of the epithelium, in the absence of Bowman's glands and their secretion.

Eyes.

The eye (Pl. 13, fig. 60) is in an embryonic condition, roughly comparable with that of the late eleven-day embryo of the Opossum (McCrady, *l.c.cit.*) and that of the rabbit embryo of eleven and a half to twelve days.

The secondary optic vesicle is established and consists of an inner thick retinal layer (*r.l.*) and an outer thin pigment layer (*p.l.*), not yet in very intimate contact. Pigment granules have not yet appeared in the latter and only become detectable in stage D. The choroidal fissure is open and slit-like (*m.ch.f.*) and the optic stalk (*o.s.*) is tubular.

The lens (*l.*) is ovoidal, possesses a small eccentric lumen and a thick posterior and a thinner anterior wall. The mesenchyme penetrates for only a short distance around its periphery between it and the covering ectoderm, the future corneal epithelium (*c.e.*).

The distinctive feature of the eye at this stage is the presence of a relatively large closed space (*c.s.*), situated between the corneal epithelium and a roofing layer formed by the epidermis and its epitrichium (*ep.*). This is the conjunctival space or sac, the early appearance of which is specially noteworthy. Examination of earlier stages shows that the epidermis rises up as a thickened rim around the site of the optic vesicle and gradually closes in from all sides over it but so as to leave a cavity, the conjunctival space, floored by the original ectoderm, the future corneal epithelium, and roofed by the thickened epidermis and its epitrichial layer. In the new-born, a minute central aperture may still be present in the roofing layer so formed.

The presence of a slit-like conjunctival sac was observed by Levi (1926) in the developing eye of a 15 mm. pouch-young of *Didelphis* and Keibel (1928) showed that it is present in the pouch-young of *P. obesula* from the 15 mm. stage (the earliest he examined) onwards. The early overgrowth of the epidermis, with the resulting formation of the conjunctival space provides an efficient protection for the developing eye.

It should be emphasized that the definitive eye-lids are not yet formed. They arise later (already in stage D) by the penetration of the mesenchyme from above and below between the roofing epidermal layer and the lining of the conjunctival sac (cf. Keibel, *loc. cit.*, figs. 3-6).

The corneal epithelium (*c.e.*) is formed by a layer of small cubical cells which is continuous at its periphery with a very thin endothelial-like layer which lines the remainder of the conjunctival space.

The primordium of the naso-lachrymal duct is represented by a solid cord of cells (*nl.d.*) which fails to reach the lining of the nasal cavity and curiously enough, it seems to have lost its original continuity with the epithelium at the dorsal corner of the conjunctival space.

Auditory vesicles.

The auditory vesicles (Pl. 12, fig. 56; Pl. 13, fig. 57) are at the stage of those of McCrady's stage 31 (second half of the 11th day) of the Opossum (Larsell, McCrady & Zimmerman, 1935) and of the human embryo of 9 mm. (Streeter, 1907).

Each vesicle appears as a roughly ovalish, dorso-ventrally elongated, undivided sac in which may be distinguished a larger dorsal portion from which arise the primordia of the semi-circular canals and the endolymphatic duct and an antero-ventral, less extensive and rather narrower portion from which the cochlear primordium projects very slightly forwards. The former represents the utricular portion of the membranous labyrinth and the latter, its sacculo-cochlear portion.

This latter portion (fig. 56, *c.p.*) reaches down almost to the level of the basal plate and is continued forwards laterally to the basal plate as a very short blindly ending tubular process, which reaches a length of about 0.06 mm. in series 5, 20.10.VII.02 but less in other specimens. This process and the pouch from which it arises together represent the cochlear primordium.

Dorsally, the utricular portion of the vesicle is prolonged into a wide diverticulum which narrows upwards and which we interpret as the primordium of the anterior (superior) semi-circular canal (*s.sc.*).

Below it and above the posterior extremity of the cochlear pouch, the lateral utricular wall is produced into a very distinct wide outbulging, bounded below by a ridge-like fold of the wall, which becomes closed off to form a very short cul-de-sac (about 0.04 mm. in length in the above-mentioned series). This we regard as the primordium of the horizontal semi-circular canal (fig. 57, *h.sc.*). The caudal outbulging of the vesicle behind the latter and which forms the continuation of the primordium of the anterior semi-circular canal would seem to represent that of the posterior canal.

In the slightly older series of stage A (28.8.98), the antero-ventral wall of the utricular portion of the vesicle, at the level of the primordium of the horizontal canal, is definitely thickened over a localized area and exhibits a differentiation into a superficial zone, containing a single row of rounded or oval nuclei and a deep zone, with crowded nuclei. This would appear to represent the primordium of the utricular macula.

The endolymphatic duct (fig. 57, *e.d.*) arises from the utricular portion of the vesicle, on the medial side of the base of the primordium of the anterior canal and passes upwards medially to the same as an at first, narrow but antero-posteriorly wide canal. It soon expands above to form a small saccule which lies in broad contact with the layer of condensed mesenchyme below the epidermis.

In the new-born Opossum (McCrady, *loc. cit.*, p. 193, fig. 63 (35)), the auditory vesicle is greatly in advance of that of the new-born *Dasyurus* in as much as the semicircular canals with their ampullae are established and "the cochlear duct has grown out to about one-half turn".

The auditory ganglion is still a single, relatively large mass, but is distinguishable into a much thicker and more massive, medio-ventral (cochlear) portion and a dorso-lateral thinner (vestibular) portion.

SUMMARY.

The biology of the pouch-young (mammary foetus) is considered in a graded series of stages of *Dasyurus* commencing with the new-born, still unattached young and ending with the fully developed animal at the time it leaves the maternal

pouch (at the age of 4 to 4½ months) and capable of fending for itself. The series has been divided for convenience into seventeen stages, labelled A–P, and the growth, external appearances and eruption of teeth has been fully considered.

The problem of the migration of new-born young to the pouch, their attachment to the nipples, and the mode of lactation and its duration have been considered, together with some comment of the supposed mammary compressor action of the cremaster muscles.

The internal structure of the new-born *Dasyurus* has been described in detail, special emphasis being laid on the precocious development of certain structures which are considered necessary adaptational machinery for the insurance of survival of the young in its unusual environment and more particularly those features required for the sole purpose of ensuring its safe arrival in the pouch, its becoming attached to a nipple and the certitude of its receipt of milk without hindrance to its respiration.

Notable at birth are (i) the relatively advanced state of the fore-limbs, (ii) the presence of deciduous claws upon the manual digits and their later replacement by definitive claws, (iii) the presence of the oral shield as a specialization upon the muzzle, (iv) the unique cervical swelling, (v) special features of the tongue and larynx, with the intranarial epiglottis (vi) the reptilian state of the lungs, (vii) the advanced condition of the stomach and duodenum compared with the rest of the gut, (viii) the state of development of brain and sense organs, the olfactory parts being especially forward in development, together with those parts of the nervous system necessary for controlling the movements of the fore-limb, sucking and respiratory movements, (ix) the indifferent state of the gonads.

Throughout comparison has been made with the new-born of other marsupials, so far as these are known, and features common to them all or peculiar to *Dasyurus* have been pointed out.

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PLATE 1.

PLATE 1.

G.L. and H.L. signify greatest length and head length respectively.

- Fig. 1. Stage η , uterine embryo shortly before birth, with the shrivelled remains of the allantois at its caudal end. G.L. about 5.5 mm. $\times 10$.
- Fig. 2. Stage A. New-born, unattached young. G.L. about 5.6 mm. $\times 11.8$.
- Fig. 3. Stage B. Lateral view of attached pouch-young, several hours old. G.L. 6 mm. $\times 9$.
- Fig. 4. Stage B. Ventro-lateral view of another specimen. $\times 10.8$.
- Fig. 5. Stage C. Pouch-young about 30 hours old, attached to nipple. G.L. 6 mm. \times about 11.
- Fig. 6. Stage D. About three days old. G.L. 7 mm. $\times 9.3$.
- Fig. 7. Stage E. Five-six days old. G.L. 8 mm. $\times 9.25$.
- Fig. 8. Stage F. About seven days old. G.L. 8.5-9 mm. $\times 9.7$.
- Fig. 9. Stage G. About ten days old. G.L. 10 mm. H.L. 6.5 mm. $\times 8$.

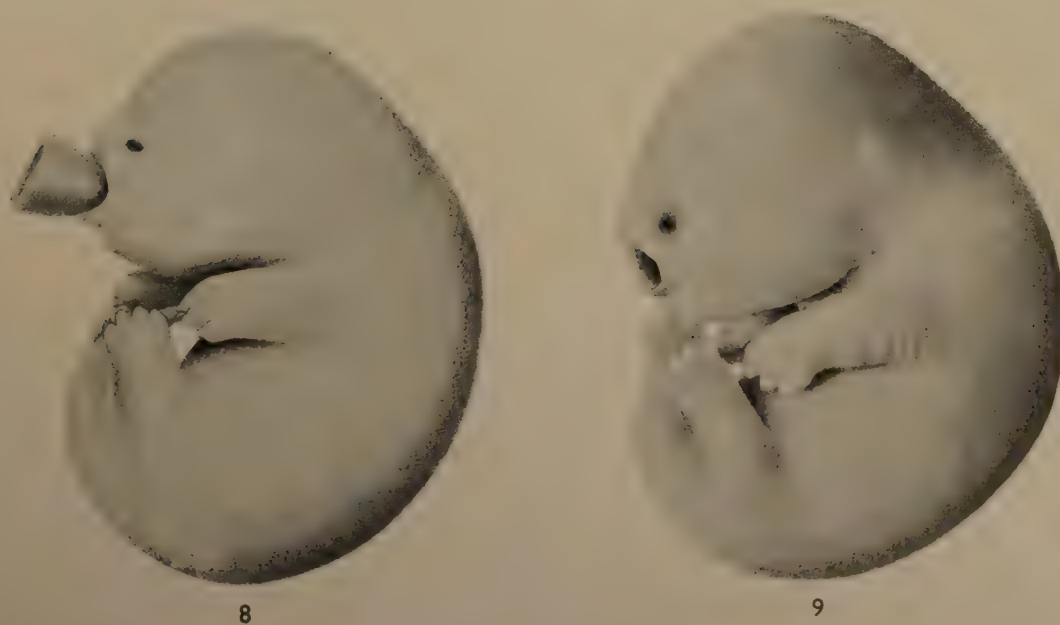
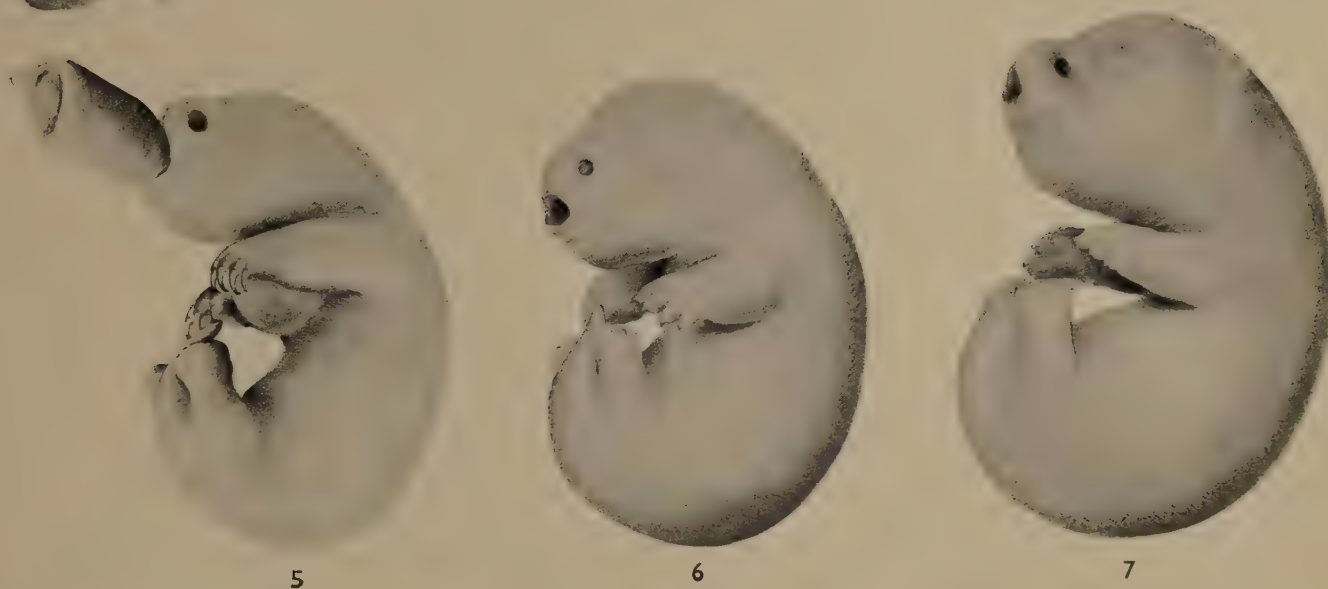


PLATE 2.

PLATE 2.

G.L., H.L. and D.C.L. signify greatest length, head length and dorsal curve length respectively.

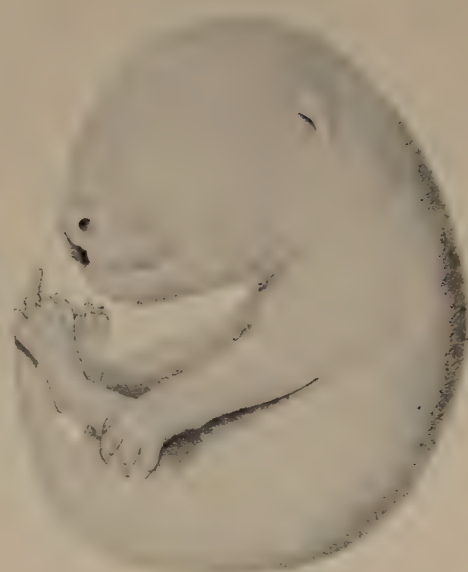
- Fig. 10. Stage H. About fourteen days old. G.L. 13·5 mm. H.L. 8 mm. $\times 6$.
Fig. 11. Stage I. About nineteen days old. G.L. 16·5 mm. H.L. 10 mm.
D.C.L. 3·8 cm. $\times 4$.
Fig. 12. Stage J. About twenty-five days old. G.L. 20 mm. H.L. 12·5 mm.
D.C.L. 4·75 cm. $\times 3\cdot 8$.
Fig. 13. Stage J'. About thirty-five days old. G.L. 24 mm. H.L. 13·5 mm.
D.C.L. 5·2 cm. $\times 3\cdot 1$.
Fig. 14. Stage K. About six weeks old. G.L. 29 mm. H.L. 18 mm. D.C.L. 6 cm.
 $\times 2\cdot 5$.
Fig. 15. Stage L. About seven weeks old. G.L. 42 mm. H.L. 21 mm. D.C.L.
7·1 cm. \times nearly twice.
Fig. 16. Stage M. Just over two months old. G.L. 59 mm. H.L. 30 mm.
D.C.L. 8·6 cm. $\times 1\cdot 4$.
Fig. 17. Stage N. Barely two and a half months old. G.L. 65 mm. H.L. 34 mm.
D.C.L. 10 cm. $\times 1\cdot 4$.



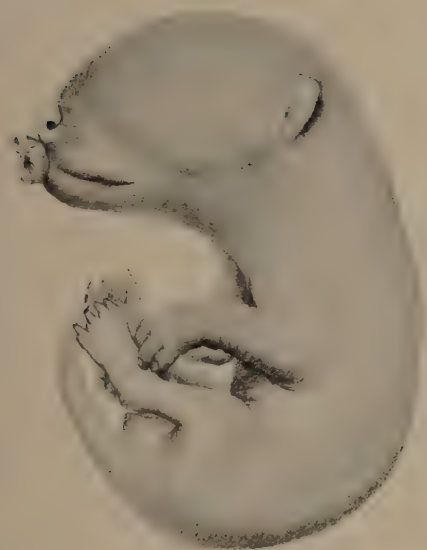
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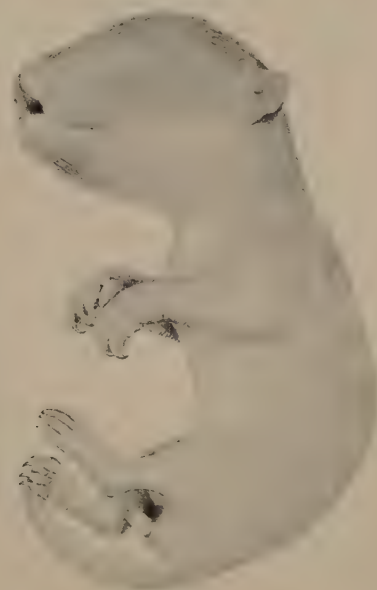
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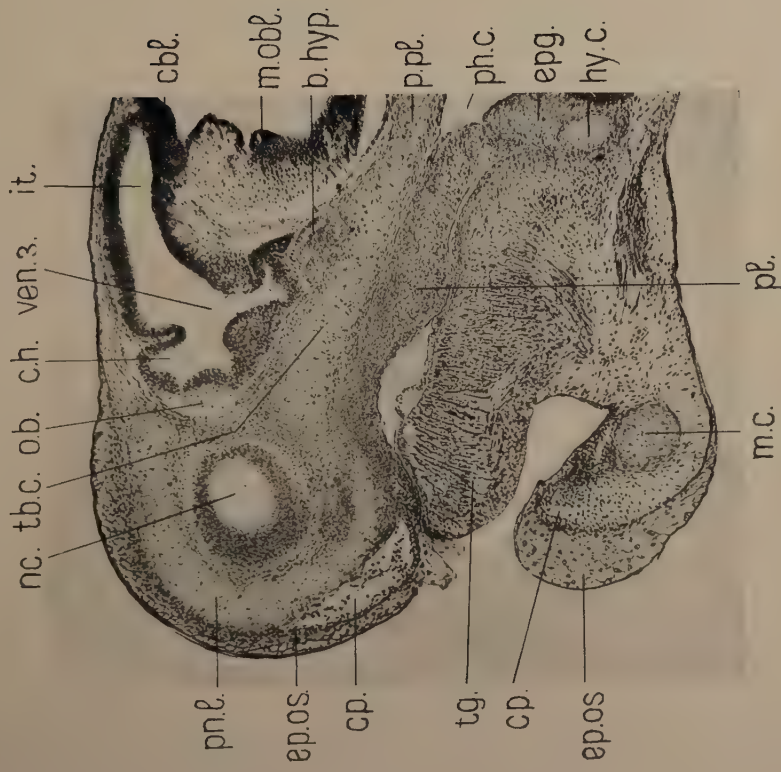
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PLATE 3.

PLATE 3.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

- Fig. 18. Stage A. L.S. (5-3-2). Sagittal section through the head, showing especially the thickened epidermis of the oral shield (*ep.os.*) and the underlying enlarged capillaries (*cp.*), also the brain, tongue (*tg.*) and palate (*pl.*), (*c.h.*) cerebral hemisphere, (*o.b.*) olfactory bulb, (*ven. 3*) 3rd ventricle, (*it.*) iter, (*obl.*) lateral connection of median cerebellar primordium with the medulla oblongata (*m.obl.*), (*b.hyp.*) buccal hypophysis, (*p.pl.*) parachordal cartilage, (*tb.c.*) trabecula, (*pn.l.*) prenasal lamina, (*m.c.*) Meckel's cartilage, (*hy.c.*) hyoid cartilage, (*epg.*) epiglottis, (*ph.c.*) pharyngeal cavity, (*nc.*) nasal cavity. $\times 67$.
- Fig. 19. 20.10.VIII.02. T.S. (15-3-1). Oblique horizontal section through the snout, showing the thickened epidermis of the oral shield (*ep.os.*) and the thick epitrichium covering it (*ept.*), the underlying capillaries (*cp.*), the prenasal lamina (*pn.l.*), the nasal septum (*n.s.*), the olfactory epithelium (*o.ep.*) and the external naris (*e.n.*). $\times 130$.
- Fig. 20. 1.VII.05. L.S. (6-6-1). Median sagittal section, showing the relations and structure of the cervical swelling (*cs.*), (*st.*) sternum. $\times 60$.
- Fig. 21. 1.VII.05. L.S. (6-6-1). Median sagittal section showing the epiglottis (*epg.*), intra-pharyngeal in position, and its relation to the soft palate (*vp.*), the ventral margin of which projects into the glosso-epiglottic sulcus (*gep.s.*), (*bc.*) buccal cavity, (*cr.c.*) cricoid cartilage, (*cs.*) cervical swelling, (*gl.*) glottis, (*hy.c.*) hyoid cartilage, (*l.c.*) laryngeal cavity, (*nph.*) nasopharynx, (*oes.*) oesophagus, (*ph.c.*) pharyngeal cavity, (*pp.ft.*) termination of the palato-pharyngeal folds, (*tr.*) trachea. $\times 126$.



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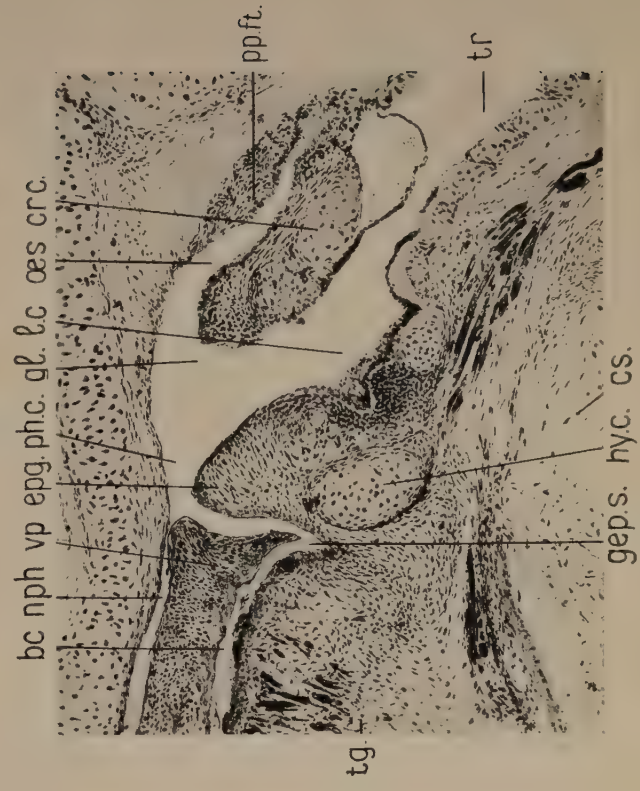
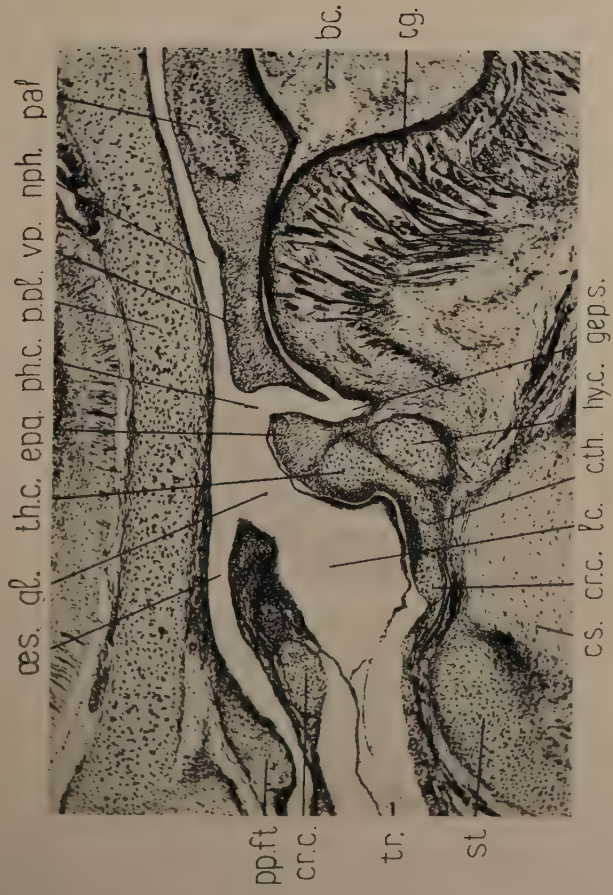


PLATE 4.

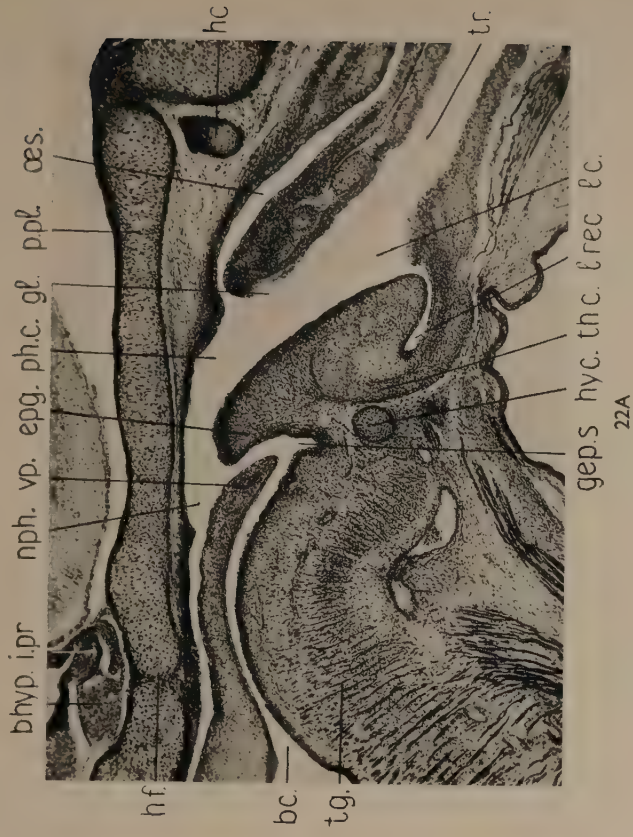
PLATE 4.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

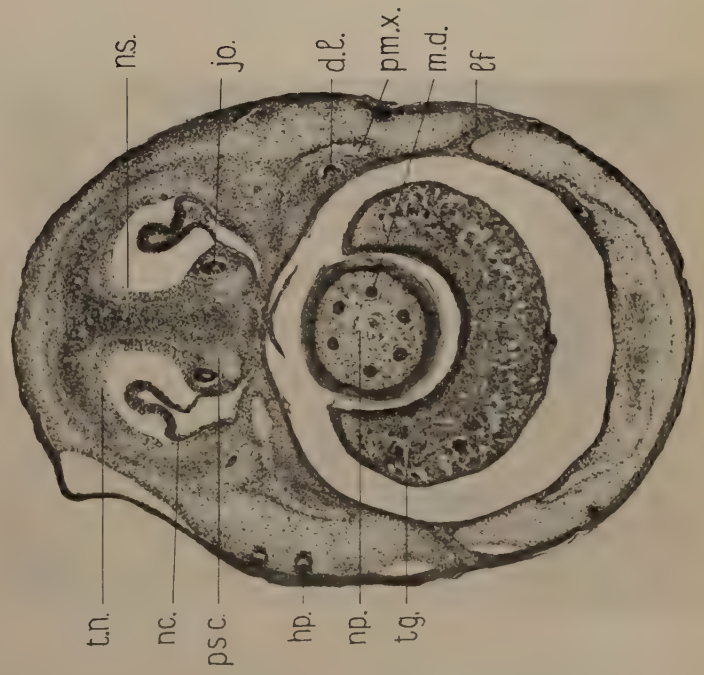
- Fig. 22. Stage D. 24.VII.01. L.S. (7-5-2). Median sagittal section similar to the preceding but showing better the relations of the posterior part of the tongue (*tg.*) to the adjoining parts. Additional lettering: (*p.pl.*) para-chordal plate, (*pal.*) palatine ossification, (*st.*) sternum, (*th.c.*) thyroid cartilage, (*c.th.*) thyroid cornu. $\times 110$.
- Fig. 22a. *T. vulpecula*. Stage XXIV. Uterine embryo. G.L. 13.5 mm. H.L. 6.5 mm. L.S. (3-1-7). Sagittal section showing the epiglottis (*epg.*) projecting forwards into the naso-pharynx (*nph.*) and overlying the hinder portion of the soft palate (*vp.*) which thins back to terminate in a rounded margin, in the glosso-epiglottic sulcus (*gep.s.*), (*b.hyp.*) buccal hypophysis, (*hc.*) hypocentrum below the atlanto-occipital joint, (*h.f.*) hypophysial foramen, (*i.pr.*) infundibular process, (*l.rec.*) laryngeal recess. Other lettering as in figs. 21 and 22.
- Fig. 23. Stage D. T.S. (10-5-1a). T.s. through the anterior part of the head, to show the nipple (*np.*) with its six milk-ducts (*m.d.*), *in situ* in the buccal cavity and partially enclosed by the deeply grooved anterior portion of the tongue (*tg.*). Note also the line of fusion (*lf.*) of the epidermis of the lips. (*d.l.*) dental lamina, (*hp.*) hair (vibrissa) primordium, (*jo.*) Jacobson's organ, (*nc.*) nsaal cavity, (*n.s.*) nasal septum, (*t.n.*) tectum nasi, (*pmx.*) premaxillary ossification, (*ps.c.*) paraseptal cartilage. $\times 67$.
- Fig. 24. Stage B. L.S. (3-3-3). L.s. through the tip of a digit of the manus, showing the recurved claw (*dc.*) continuous with the epitrichial layer (*ept.*) of the epidermis, the tendon (*ext.t.*) of the extensor muscle, the flexor muscle (*fl.m.*) and the beginning of its tendon (*fl.t.*) and the phalangeal procartilage (*ph.c.*). $\times 127$.



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22A



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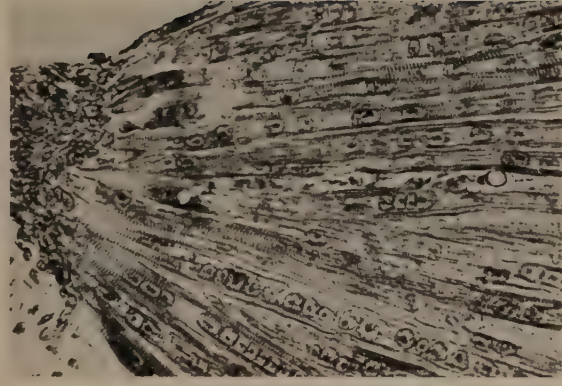
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PLATE 5.

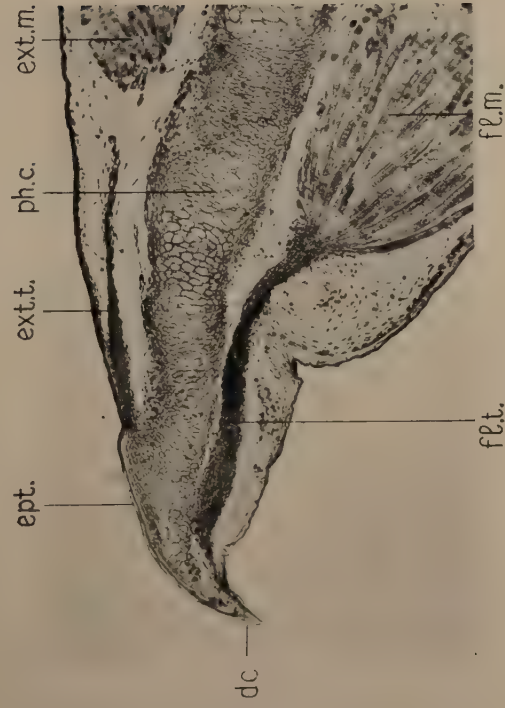
PLATE 5.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

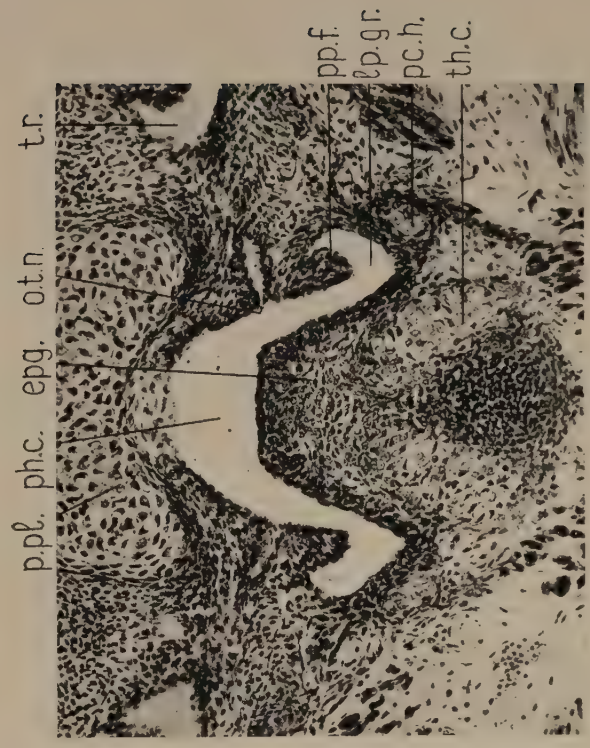
- Fig. 25. Stage B. L.S. (1-3-3). Similar section to the preceding but showing the tendon (*fl.t.*) of the flexor muscle (*fl.m.*) cut along its length, (*ext.m.*) extensor muscle. Other lettering as in preceding figure. $\times 103$.
- Fig. 26. 20.10.VII.02. L.S.A. (7-4-4). Similar section to the preceding showing the claw at its maximum flexure. Note the terminal portion of the phalangeal procartilage is also bent round with it as is more clearly seen in the succeeding sections of the series. $\times 127$.
- Fig. 27. Stage B. L.S. (8-2-1). L.s. of the flexor muscle of the claw, showing the muscle fibres with centrally situated nuclei and the cross-striation of their constituent fibrillae. $\times 400$.
- Fig. 28. 20.10.VII.02. T.S.5. (15-5-1). T.s. passing through the epiglottis (*epg.*) and pharynx (*ph.c.*), (*lp.gr.*) laryngo-pharyngeal groove, (*o.t.r.*) opening of tubo-tympanic recess (*t.r.*) into pharynx, (*p.pl.*) parachordal (basal) plate, (*pc.h.*) posterior cornu of hyoid, (*pp.f.*) palato-pharyngeal fold, (*th.c.*) thyroid cartilage (paired). $\times 147$.



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PLATE 6.

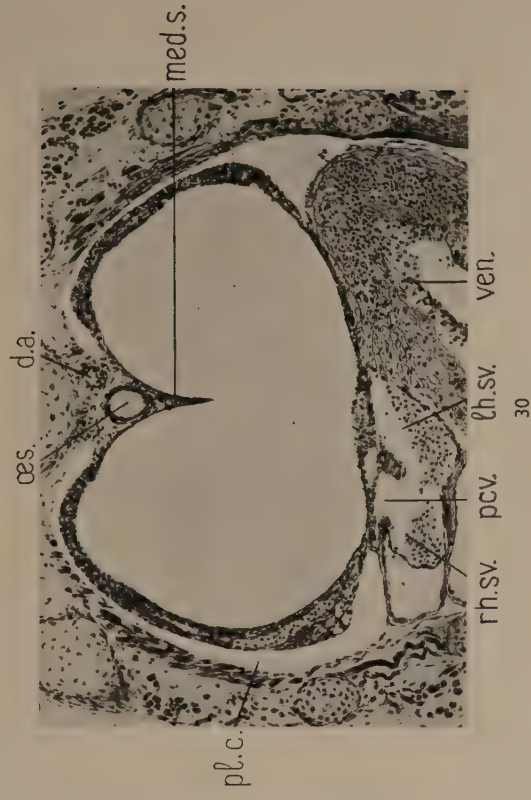
PLATE 6.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

- Fig. 29. T.s. (7-6-1). Shortly behind preceding figure and passing through the glottis (*gl.*), (*a.c.*) arytenoid cartilage, (*cr.c.*) cricoid cartilage, (*c.th.*) cornu of thyroid cartilage, (*gn.p.*) ganglion petrosum, (*l.c.*) laryngeal cavity. Other lettering as in preceding figure. $\times 214$.
- Fig. 30. 20.10.VII.02. T.S. 5 (19-5-2). T.s. through the lungs, showing the "common pulmonary cavity" formed by the cavities of the incipient bronchi medianly and the lung-cavities laterally. Below the oesophagus (*oes.*), the mediastinal septum (*med.s.*) is beginning to appear. (*d.a.*) dorsal aorta, (*pl.c.*) pleural cavity, (*pcv.*) post-caval vein opening into right horn of sinus venosus (*rh.sv.*). (*lh.sv.*) left horn of sinus venosus. $\times 87$.
- Fig. 31. T.s. (16-6-2). Shortly behind the preceding figure, showing the large right lung (*r.l.*) and the smaller left lung (*l.l.*) with the ventricular portion of the heart (*ven.*) projecting upwards and to the left, below it. (*div.*) diverticulum of lung-cavity, (*r.ch.p.*) primordium of respiratory chamber, (*pl.c.*) pleural cavity, (*spt.*) septal ingrowth, (*pcv.*) postcaval vein attached to the pleuro-pericardial membrane (*s.plp.*). $\times 87$.
- Fig. 32. Stage B. L.S. (1-1-2). L.s. of the lung, showing its continuous cavity and the septal ingrowths (*spt.*) separating the large respiratory chambers (*r.ch.*). $\times 73$.



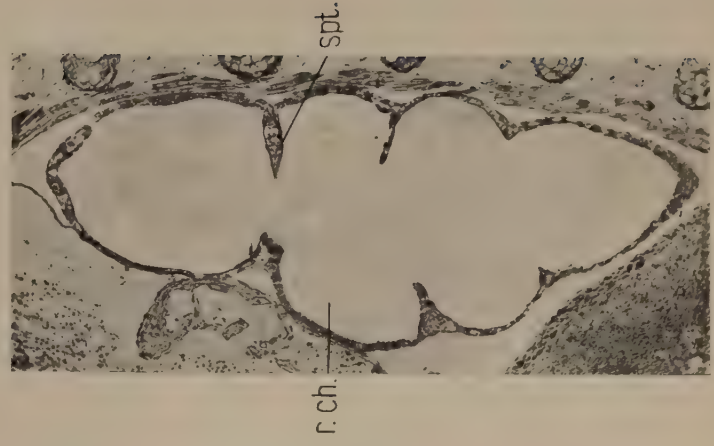
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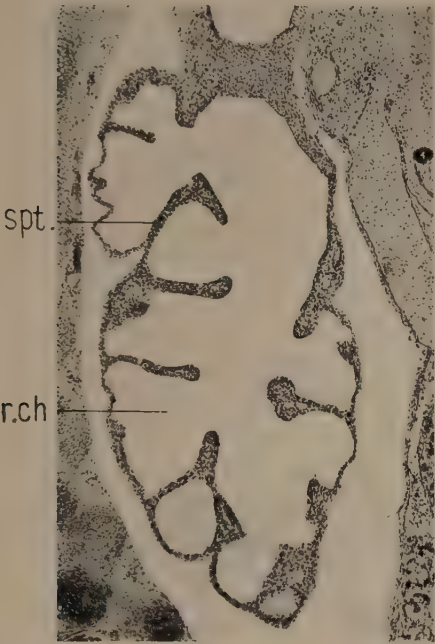
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PLATE 7.

PLATE 7.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

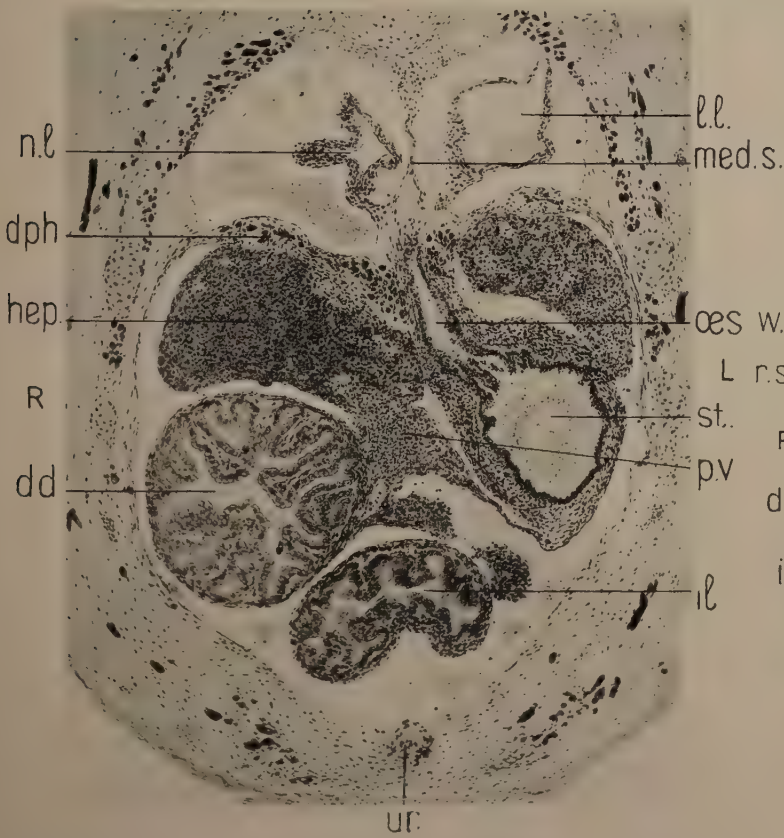
- Fig. 33. Stage F. L.S. (1-2-3). L.s. of the lung showing the now well-developed septal ingrowths (*spt.*) and the respiratory chambers (*r.ch.*). $\times 45$.
- Fig. 34. 20.10.VII.02. L.S.A (7-3-4). Sagittal section showing the constitution of the diaphragm. (*dp.m.*) muscle fibres of the dorsal pillar. (*tr.m.*) transverse muscle fibres, (*s.pp.*) pericardio-peritoneal septum, (*s.plp.*) pleuro-pericardial septum, (*hep.*) liver, (*div.*) diverticulum of lung, (*ven.*) ventricle. $\times 103$.
- Fig. 35. 1.VII.05. T.S. (12-1-3). T.s. through the trunk at the level of the opening of the oesophagus (*oes.*) into the stomach (*st.*) situated on the left side (right in the figure). (*dd.*) duodenum, (*il.*) ileum, (*hep.*) liver, (*p.v.*) portal vein, (*dph.*) diaphragm, (*r.l.*) and (*l.l.*) right and left lungs, (*med.s.*) mediastinal septum, (*ur.*) urachus. $\times 93$.
- Fig. 36. 20.10.VII.02. T.S.5 (2-2-3). T.s. through the trunk, caudal to the level of the preceding figure and cranial to the subcardinal anastomosis. (*dd.*) duodenum, with villous folds, (*oil.*) opening of ileum (*il.*) into large intestine. (*l.i.*) large intestine, (*mesn.*) mesonephros, (*w.d.*) Wolffian duct, (*csp.*) cortical suprarenal primordium, (*r.sc.*) right subcardinal vein, (*mes.a.*) mesenteric artery, (*umb.*) umbilicus. $\times 93$.



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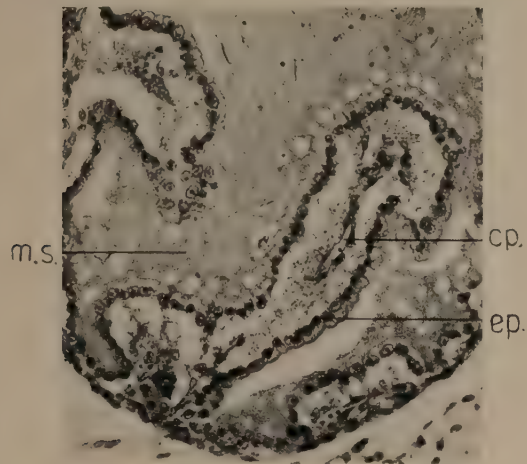
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PLATE 8.

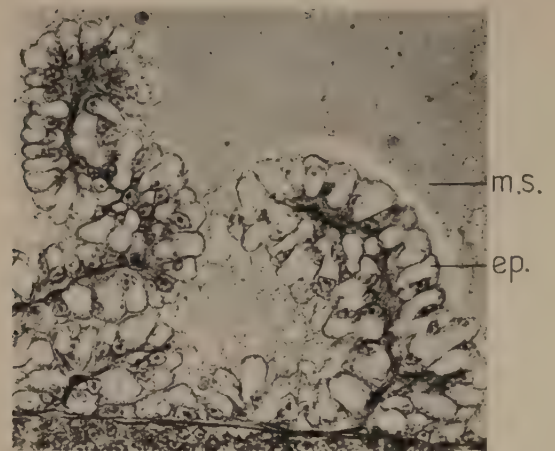
PLATE 8.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

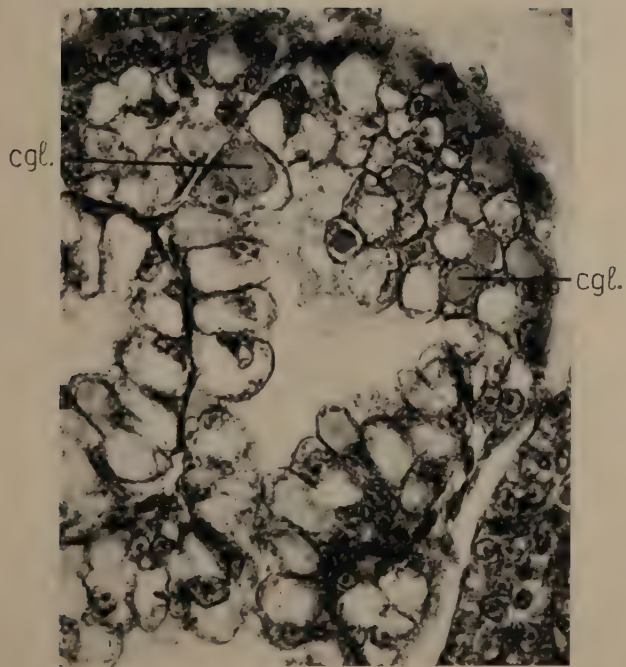
- Fig. 37. Stage A. L.S. (8-3-2). Section of duodenum, showing a villous fold with its covering epithelium (*ep.*) and a central capillary (*cp.*), (*m.s.*) mammary secretion. $\times 173$.
- Fig. 38. Stage B. L.S. (10-4-2). Section of duodenum showing its villous folds and their covering epithelium (*ep.*) now composed of greatly enlarged cells. $\times 220$.
- Fig. 39. Stage B. L.S. (7-5-2). Section of duodenum showing the enlarged epithelial cells forming its lining, many of them containing a dense coagulum (*cgl.*). $\times 380$.
- Fig. 40. 20.10.VII.02. T.S. (12-4-3). T.s. passing through the cranial portion of the atrial region of the heart, (*r.atr.*), (*l.atr.*) right and left atria, (*s.pr.*) septum primum, and (*pf.*) perforation in the same, (*s.sp.*) septum spurium, (*rh.sv.*) right horn, sinus venosus, with the right precaval vein (*r.pv.*) opening into it, (*l.pv.*) left recaval vein, (*b.c.*) bulbus cordis, (*ec.A.*) and (*ec.B.*) endocardial cushions A and B, (*d.a.*) dorsal aorta, (*oes.*) oesophagus, (*tr.*) trachea. $\times 103$.



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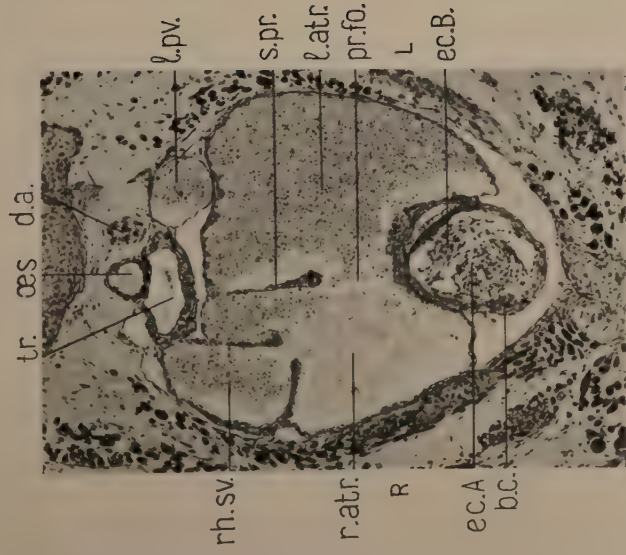
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PLATE 9.

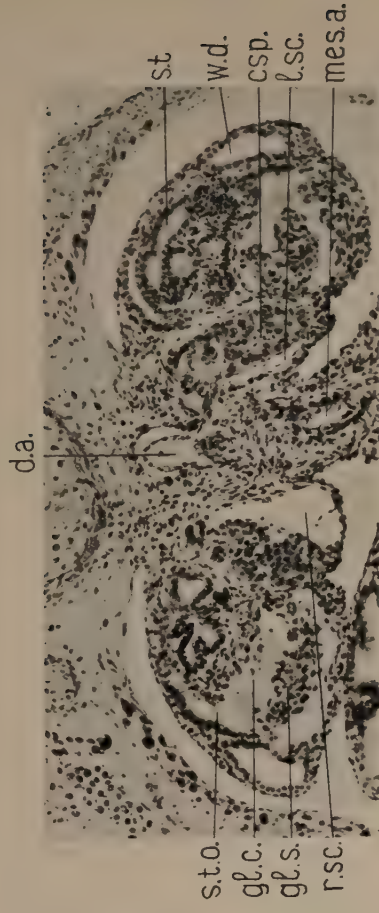
PLATE 9.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

- Fig. 41. Section (3-5-3). 0.072 mm. (nine sections) behind preceding figure. (*pr.fo.*) primary foramen ovale, (*s.pr.*) septum primum with a minute perforation just below its dorsal attachment. (*rh.sv.*) right horn, sinus venosus, opening into the right atrium (*r.atr.*), between the right and left venous valves. Other lettering as in preceding figure. $\times 103$.
- Fig. 42. 20.10.VII.02. T.S. 5 (2-2-3). T.s. passing through the mesonephroi and the cortical suprarenal primordia (*csp.*), cranial to the subcardinal anastomosis. (*w.d.*) Wolffian duct, (*s.t.*) secretory tubule, (*s.t.o.*) opening of secretory tubule into a glomerular cavity (*gl.c.*), (*gl.s.*) glomerular septum, (*r.sc.*) and (*l.sc.*) right and left subcardinal veins. (*d.a.*) dorsal aortal. (*mes.a.*) mesenteric artery. $\times 147$.
- Fig. 43. T.s. (4-3-3), through the mesonephroi, shortly behind the preceding figure and immediately behind the subcardinal anastomosis. (*c.t.*) collecting tubule opening into the Wolffian duct (*w.d.*), (*s.t.*) secretory tubule, (*g.r.*) gonadal ridge, (*r.pc.v.*) right posterior cardinal vein and (*l.pc.v.*) left vein opening widely below into the left subcardinal vein (*l.sc.*), (*r.sc.*) right subcardinal vein. Other reference figures as in preceding figure. $\times 180$.
- Fig. 44. 1.VII.05. T.S. (6-3-3). Horizontal section through the mesonephros. (*gl.c.*) glomerular cavity, (*gl.s.*) glomerular septum, (*s.t.*) secretory tubule, (*s.t.o.*) opening of secretory tubule into glomerular cavity, (*csp.*) cortical suprarenal primordium. $\times 193$.



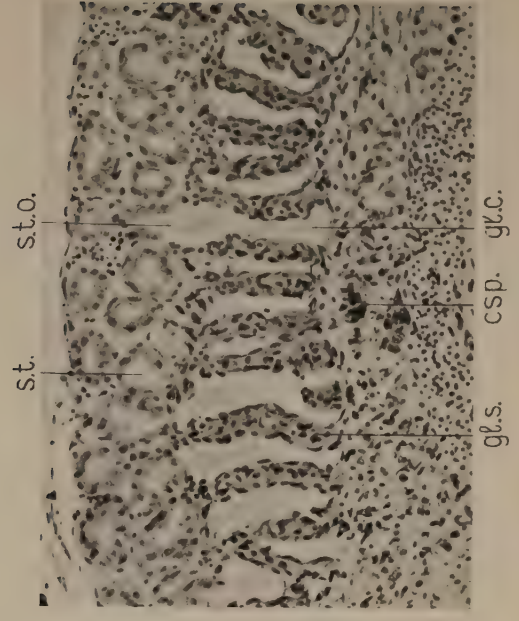
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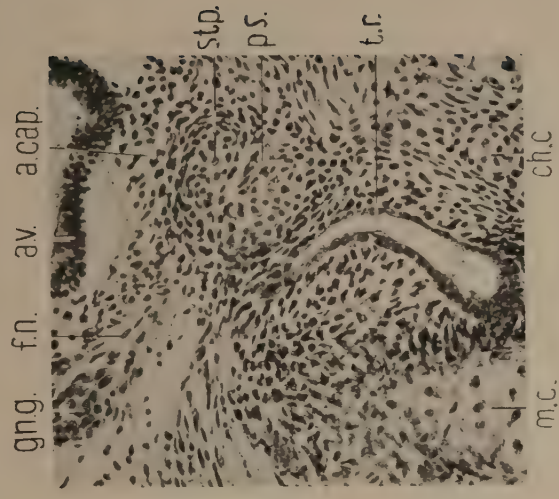
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PLATE 10.

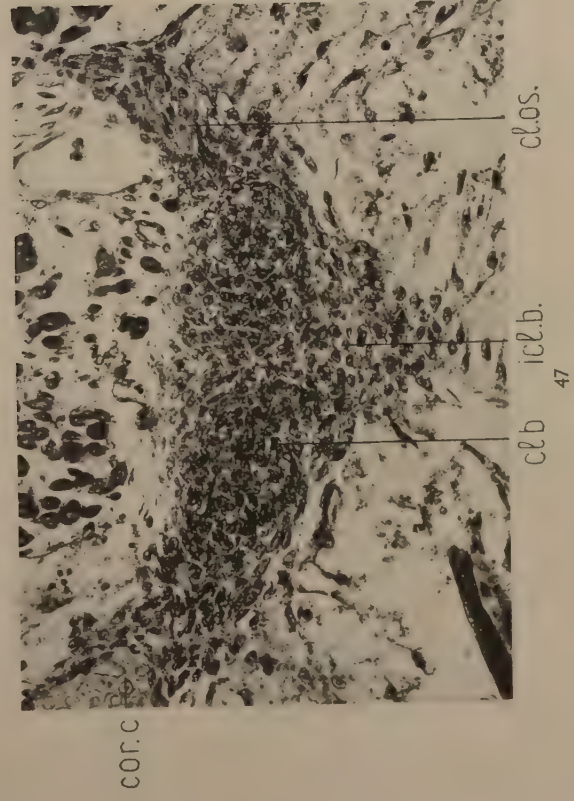
PLATE 10.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

- Fig. 45. 1.VII.05. (L.S.) (2-2-2). Sagittal section showing the primordium of the incus (*inc.*) overlying the upper end of Meckel's cartilage, the primordium of the malleus (*mp.*), (*m.c.*) Meckel's cartilage, (*a.cap.*) auditory capsule, (*f.n.*) facial nerve. $\times 213$.
- Fig. 46. 1.VII.05. (10-1-2). Sagittal section 0.08 mm. medial to the preceding figure, showing the primordium of the stapes (*stp.*) situated dorso-caudally to the upper end of the tubo-tympanic recess (*t.r.*) and with a perforating strand of mesenchyme (*ps.*) penetrating into it. (*a.cap.*) auditory capsule, (*a.v.*) floor of auditory vesicle, (*gn.g.*) geniculate ganglion, (*f.n.*) facial nerve, (*ch.c.*) cerato-hyal cartilage, (*m.c.*) Meckel's cartilage. $\times 300$.
- Fig. 47. Stage A. T.S. 7-8-2. T.s. showing the paired clavicular blastema (*cl.b.*) in the outer ends of which the clavicular ossifications (*cl.os.*) are beginning and also the median inter-clavicular blastema (*icl.b.*), (*cor.c.*) coracoid cartilage. $\times 300$.
- Fig. 48. 20.10.VII.02. T.S.5 (12-4-1). T.s. showing the buccal hypophysis, the parachordal (basal) plate (*p.pl.*), perforated by the carotid canal (*c.c.*) (on the apparent right) and continuous on each side with a ventrally recurved cartilage (*pr.a.*), representing the processus alaris and probably also the ala temporalis. (*d.l.*) and (*p.l.*) distal and proximal lobes of the buccal hypophysis, (*i.c.a.*) internal carotid artery, (*gn.sl.*) semilunar ganglion, (*pn.c.*) posterior nasal canal, (*r.pl.*) median ridge of hard palate. $\times 133$.



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PLATE II.

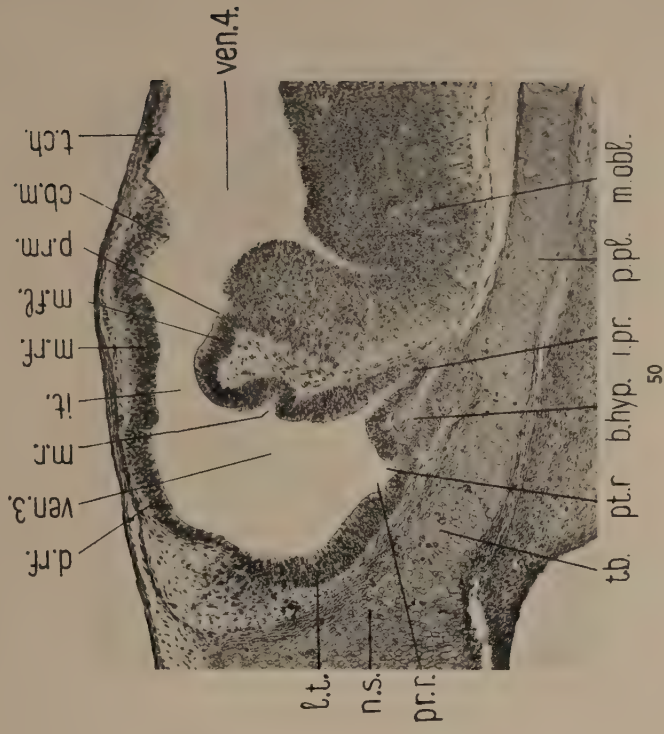
PLATE 11.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

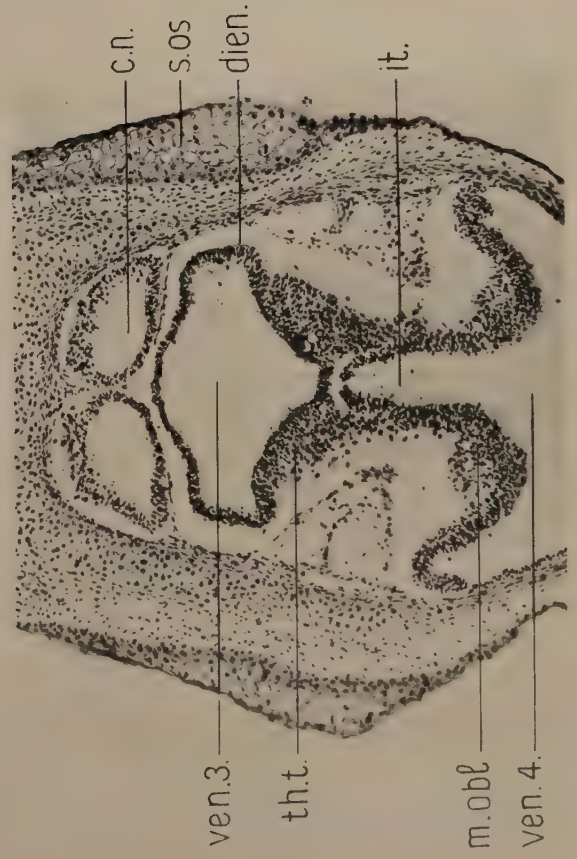
- Fig. 49. Stage A. L.S. (10-3-2). Slightly oblique sagittal section through the brain. (*b.hyp.*) buccal hypophysis, (*c.h.*) cerebral hemisphere, (*cb.m.*) median cerebellar primordium, (*d.rf.*) diencephalic roof, (*f.pl.*) floor-plate of medulla oblongata, (*it.*) iter, (*i.pr.*) infundibular process, (*l.t.*) lamina terminalis, (*m.fl.*) mesencephalic floor, (*m.obl.*) medulla oblongata, (*m.r.*) mammillary recess, (*n.s.*) nasal septum, (*o.b.*) olfactory bulb, (*p.pl.*) para-chordal (basal) plate, (*p.rm.*) plica rhombomesencephalica, (*p.t.*) posterior tubercle, (*pr.r.*) preoptic recess, (*pt.r.*) postoptic recess, (*tb.*) trabecula, (*t.ch.*) tela choroidea, (*ven.3*) and (*ven.4*) 3rd and 4th centricles. $\times 113$.
- Fig. 50. Stage B. L.S. (1-3-2). Sagittal section (nearly median) through the brain, showing especially the entire extent of the lamina terminalis (*l.t.*). Lettering as in the preceding figure. $\times 113$.
- Figs. 51-54. 20.10.VII.02. Illustrate four horizontal sections through the brain at successive levels, fig. 51 being the most dorsal. The preservation of the brain, in this series, is not perfect but is sufficiently good to show its general morphology.
- Fig. 51. (5-2-1). This section passes through the upwardly projecting portions of the two cerebral hemispheres (*c.h.*), the diencephalon (*dien.*), the mesencephalon (*it.*) and the medulla oblongata (*m.obl.*). Note the continuity of the ventral thalamic thickenings (*th.t.*) of the diencephalon with the ventro-lateral thickenings of the floor of the mesencephalon and the passage of these into the medulla. (*s.os.*) supra-orbital ridge, continued back from the epidermis of the oral shield. (*ven.3*) and (*ven.4*) 3rd and 4th ventricles. $\times 128$.
- Fig. 52. Section (12-2-1), 0.056 mm. below the preceding figure, showing the lateral ventricles (*c.h.*) of the cerebral hemispheres opening by wide foramina of Monro into the telencephalic portion of the 3rd ventricle (*ven.3*), and the transversely wide diencephalon (*dien.*) with the paired thalamic thickenings (*th.t.*) of its caudal (ventral) wall and the medulla oblongata (*m.olb.*) cut transversely. Note the olfactory bulbs (*o.b.*) capping the hemispheres and the telo-diencephalic folds (*pl.td.*) bounding the foramina of Monro behind and marking off the telencephalic and diencephalic portions of the 3rd ventricle. $\times 113$.



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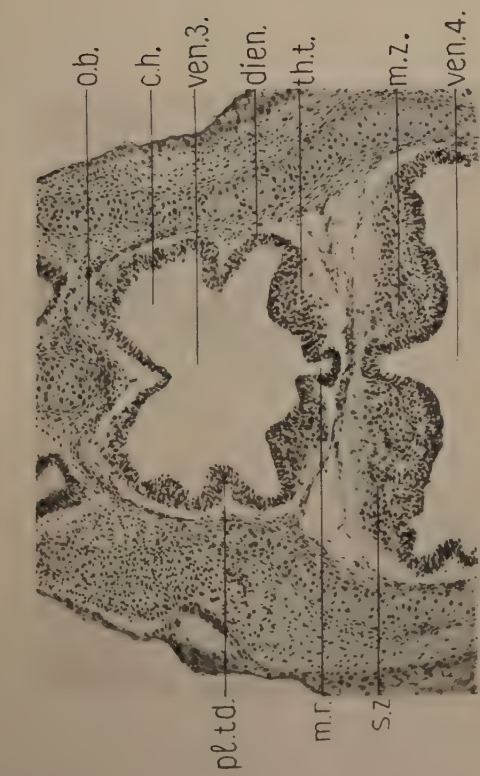
52

PLATE 12.

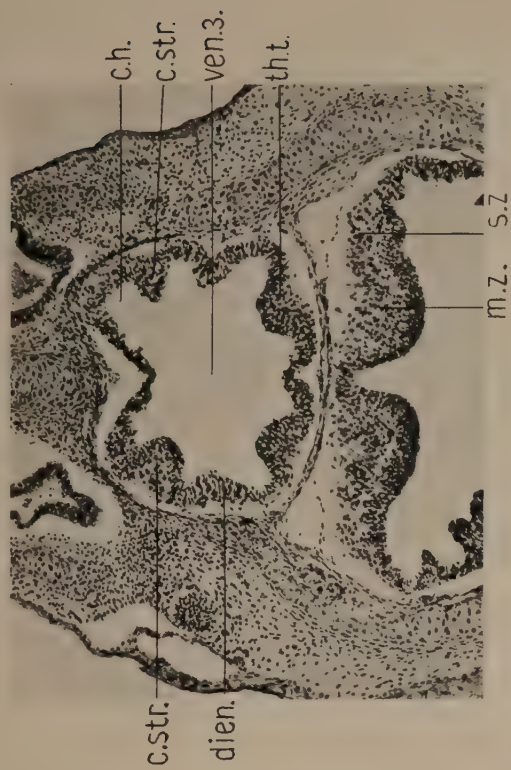
PLATE 12.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

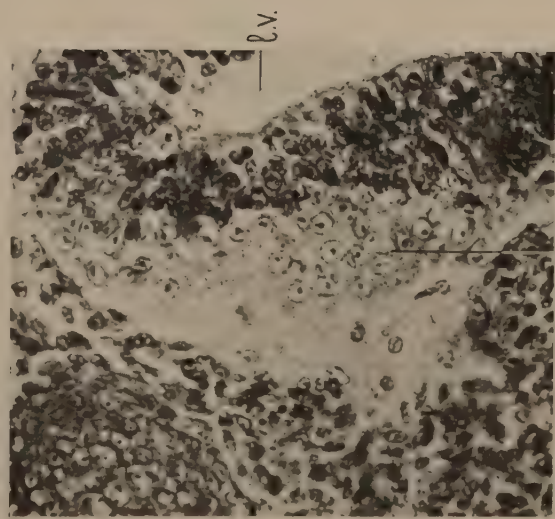
- Fig. 53. Section (4-3-1). 0.072 mm. below the preceding figure, showing the mammillary recess (*m.r.*), the well-developed ventral thalamic thickenings (*th.t.*) on either side of it, the reduced telo-diencephalic folds (*pl.td.*), the cerebral hemispheres (*c.h.*) still large and the conical olfactory bulbs (*o.b.*). In the medulla, cut transversely, the motor and sensory zones (*m.z.*) and (*s.z.*) are distinguishable. $\times 113$.
- Fig. 54. Section (10-3-1). 0.048 mm. below the preceding figure, intersecting the ventral portions of the cerebral hemispheres (*c.h.*) and showing the primordia of the corpora striata (*c. str.*). Other lettering as in fig. 53. $\times 113$.
- Fig. 55. Uterine stage ϵ . L.S. (5-3-2). Sagittal section showing the structure of the olfactory bulb (*o.b.*) and the bundle of olfactory nerve fibrillae entering it. (*l.v.*) lateral ventricle. $\times 338$.
- Fig. 56. 20.10.VII.02. T.S. (7-6-1). T.s. passing through the hind-brain and the auditory vesicles, and showing the median (*cb.m.*) and lateral (*cb.l.*) cerebellar primordia, the lateral tela choroidea (*l.tc.*), the 4th ventricle (*ven.4*), and the motor (*m.z.*) and sensory (*s.z.*) zones of the medulla. (*a.ves.*) auditory vesicle, (*s.sc.*) primordium of superior semicircular canal, (*c.p.*) cochlear pouch, (*a.cap.*) auditory capsule, (*p.pl.*) parachordal (basal) plate. $\times 77$.



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54



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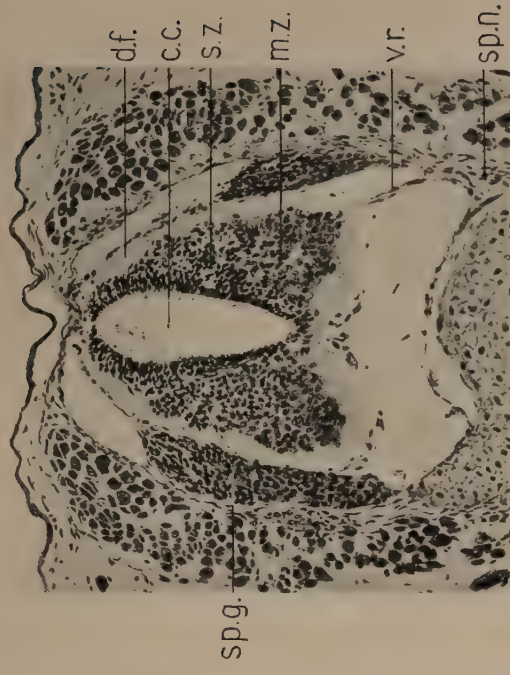
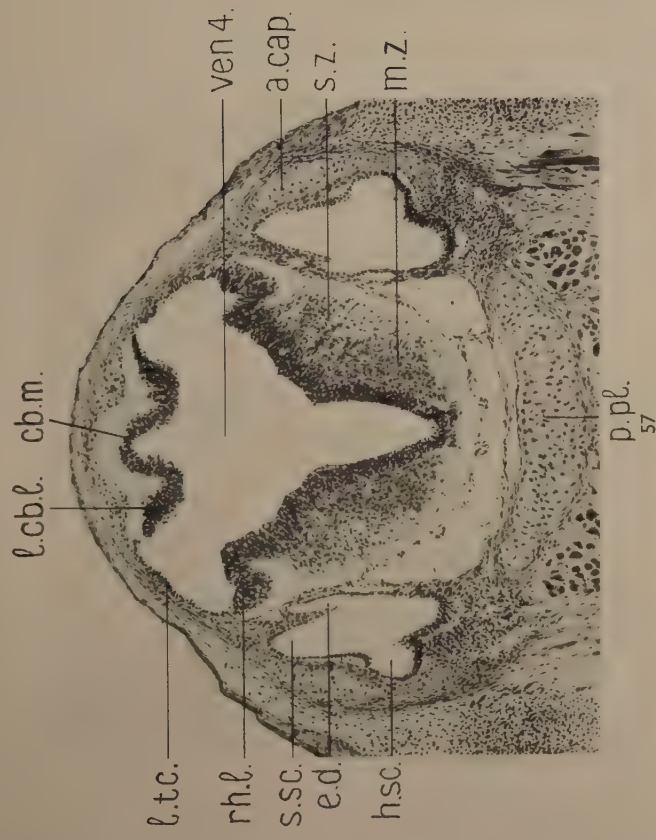
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PLATE 13.

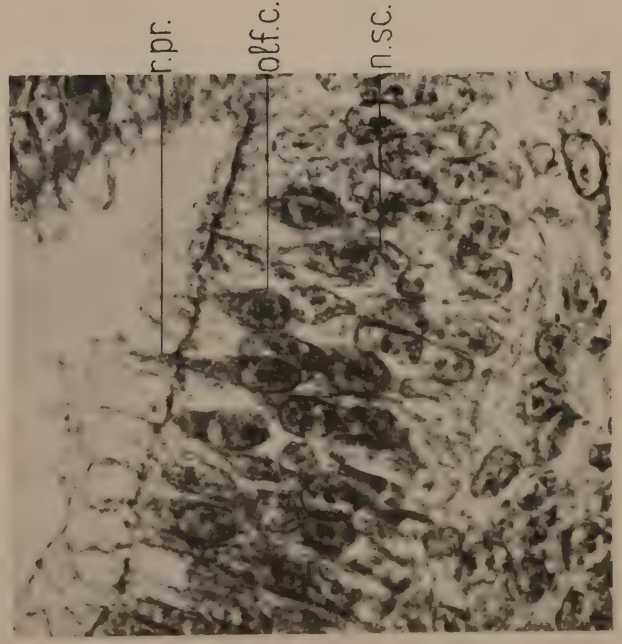
PLATE 13.

T.S. and L.S. signify transverse and longitudinal series respectively,
and T.s. and L.s. transverse and longitudinal sections.

- Fig. 57. T.s. (18-6-1). 0.11 mm. behind the preceding figure. (*rh.l.*) rhombic lip, (*e.d.*) endolymphatic duct, (*h.sc.*) primordium of horizontal semi-circular canal. Other lettering as in preceding figure. $\times 105$.
- Fig. 58. 20.10.VII.02. T.S. (7-5-2). T.s. of the spinal cord, cervical region, (*c.c.*) central canal, (*d.f.*) dorsal funiculus, (*m.z.*) motor and (*s.z.*) sensory zones of mantle layer, (*sp.g.*) dorsal root ganglion, (*v.r.*) ventral root. $\times 147$.
- Fig. 59. Stage A. T.S. (18-3-1). Section through the olfactory epithelium, showing the deeply staining pyriform olfactory cells (*olf.c.*), one with a receptive process (*r.pr.*) projecting well beyond the surface and the lighter staining nuclei (*n.sc.*) of the supporting cells. On its surface is the thin cuticular membrane with terminal bars appearing in section as minute black dots, marking the limits of the outer ends of the supporting cells. Opposite the latter are the blob-like structures referred to in the text, p. 419. $\times 953$.
- Fig. 60. 1.VII.05. T.S. (6-3-1). Section through the secondary optic vesicle, optic stalk (*o.s.*) and related parts. (*r.l.*) and (*p.l.*) retinal and pigment layers of wall of optic cup, (*m.ch.f.*) margin of choroidal fissure, (*l.*) lens, (*c.e.*) corneal epithelium, (*c.s.*) conjunctival sac, (*ep.*) epidermis, (*nl.d.*) naso-lachrymal duct. $\times 190$.



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Phylogeny in the Planorbidae.

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(With 210 figures in the text.)

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INTRODUCTION.

The Planorbidae is the most heterogenous family in the limnic Basommatophora. The natural connection between the different morphological types (in other words the phylogenetic relationship within the family as a whole) has never been worked out. The purpose of this paper is to elucidate the natural relationships within the whole family Planorbidae. In this connection it is worth mentioning that several planorbids act as intermediate hosts for many trematodes, including schistosomes. For this reason the Planorbidae has gained interest outside pure scientific zoology.

Most authors who have studied the Planorbidae have restricted their work to the conchological aspect only. Some have also made anatomical studies and a few have used their anatomical results for classification. In most cases, however, the classification has been typological rather than phylogenetical. This is true also of the most important work on Planorbidae that has been published to date (F. C. Baker's monograph 1945). Baker carefully examined very extensive collections of planorbids, but his primary results are unsatisfactory in some respects.

His material did not include representatives of the whole family, being mainly of the conventional planorbids only, i.e., planorbids of the discoidal type. Several aberrant, but important, genera were not represented. His morphological examinations are very detailed and he gives equal value to fundamental characteristics and those with only slight comparative importance. Characters of high comparative importance are often obscured by the amount of information he gives. Baker apparently failed to use the technique of sections by microtome and was therefore led into errors which he might otherwise have avoided. Further, although he was a very skilled dissector he misinterpreted the morphology of the male copulatory organ on several occasions. Section-cutting technique is the only satisfactory method in this connection, and as the male copulatory organ has proved to be particularly important as a comparative morphological feature, Baker's misinterpretations are sometimes serious.

Baker's monograph can be criticized in one other respect. He uses the characters typologically instead of making a careful assessment of their phylogenetical importance. Only a genetic approach and an evolutionary application of the characters can lead to their proper use for classification. In the present paper certain stress will be put on this basic side of the subject and the first section is devoted to the taxonomic value of the various characters in Planorbidae.

TAXONOMIC CHARACTERS IN THE PLANORBIDAE.

Species discrimination on a morphological basis is attended with certain difficulties because of the biological nature of the species. The taxonomic categories of higher rank than the species are in the main different. A genus or a family for instance is a monophyletic group separated from other groups of the same rank by a decided gap. It is particularly important that the groups are not only typologic units but phylogenetic ones. The gaps between the genera must be wide enough to let the genera appear well delimited units even when the variation in the genus is considered. The positive features which characterize the genus must indicate a definite step of evolution in a certain direction which separates the genus from other genera, and they must show that the genus is monophyletic. Features which are easily evolved, whose evolution is supported by natural selection in most environments, are less fit for genus discrimination than features without a higher or general selection value. Distinct characteristics of the radula, even if they are minute, may be more certain generic characters than considerable differences in shell form, because they are with a high degree of certainty of monophyletic origin. Aberrant or divergent features are, of course, the most certain base for characterizing genera and groups of higher category.

As already noted the most important systematic work on the Planorbidae is that by Baker (1945). Unfortunately, however, the enormous number of facts he has gathered are not critically selected in choosing taxonomic characters. He often uses as generic characters, characteristics which are not even suitable for species discrimination. Further, he seems to regard the characters more as typological ones than as comparative morphological ones with a phylogenetic

background. The usefulness of the different characters for taxonomic purposes is discussed below. Before that, however, a few words about phylogenetic trends. When comparing two forms of which one is in possession of a certain characteristic and the other not, it is often difficult to decide which of the two conditions is the primary one or the more primitive. In other words, it is often difficult to know in which direction evolution has proceeded. Sometimes it is possible to trace the direction of the evolution by comparison with other features, particularly if they form gradations or steps which can be arranged as a typological series. However, a typological series cannot simply be presumed to correspond to an evolutionary trend. Stages that appear to be successive steps in an evolutionary line may have evolved independently and lack any close genetic connection with one another. Further evidence is needed before the stages can be regarded as closely related. Moreover, if the stages belong to an evolutionary trend every step, including the first, must have been able to function and have had a functional preference over the preceding stage. Evolution must be supported by a positive selection value at every step.

Broadly speaking the usefulness of morphological features for taxonomic purposes is restricted by the intra-specific variation when used for species discrimination, and by the inter-specific variation when used for genus discrimination. The inter-generic variation is, of course, of basic importance.

Thus where species systematics is not concerned the intra-specific variation is of less importance than inter-specific variation. There are various types of intra-specific variation, viz. growth changes, seasonal variation, genotypical and ecophenotypical variation. In fixed material, artificial changes have also to be considered. Growth changes can be eliminated by considering only full grown specimens. The seasonal variation is considerable, particularly in the genitalia, and for this reason the details of the outline of the copulatory organs and the genital glands for example should not be relied upon as taxonomic characteristics. The seasonal variation also involves considerable histological changes. The genotypical variation is particularly pronounced in fresh water species where it produces microgeographic races because of the mode of evolution in fresh water habitats (see Hubendick, 1952). It is not restricted to the shell and other external features but also affects internal structures, such as the copulatory organs. A special case of genetic variation in the genitalia observed in planorbids is the "aphallie", the total absence of the male copulatory organ (*cf.* Larambergue, 1939 *a*). The ecophenotypical variation concerns in the first place external features, particularly the shell.

Artificial changes of the structures are very misleading. It is known that different fixatives cause varying degrees of shrinking and the degree of shrinking differs between various structures in the same individual. This means that many details in the outline of the organs, in the size proportions between organs as well as in certain histological structures, are not reliable comparative characters for taxonomic purposes. Measurements of structures, e.g. those belonging to the genitalia, are largely useless or may even be misleading. These artificial changes of the various structures can be eliminated by using a standard method of fixing and preservation of the material, but, for an investigation which is partly

dependent on old material from several different collections, this is impracticable, and it is therefore very necessary to select the taxonomic characters cautiously. Only those characters in which differences certainly indicate a real step in evolution can be considered.

What is said about the effect of the intra-specific variation on species discrimination is, to a wide degree, applicable to the effect of intra- and inter-specific variation on genus discrimination. The rule, that only differences which certainly indicate a real step of evolution are useful, has to be emphasized still more when dealing with the taxonomy of groups. The morphological characters and their bearing on taxonomy in Planorbidae are described in detail in the following review.

The shell was formerly the only structure used for characterizing planorbid species and groups. The shell well reflects the external form of the snail body, except the foot and head. It is undoubtedly a distinct and reliable representation of the form of the animal within. But the form varies considerably within the species; it is for instance influenced by environmental conditions that affect the respiratory behaviour which secondarily influence the growth of the surfaces available for cutaneous respiration (*cf.* Hunter, 1953). Other environmental conditions also affect the shell form, which may also vary to a considerable extent genetically. But of still more importance in this connection is the inter-specific variation within the genera, as well as the independent evolution of similar shell forms in different genera or groups. We may note that in the genus *Anisus* for instance *A. vortex* (L.) and the species of the subgenus *Bathyomphalus* are very different. On the other hand, the shell of *A. vortex* is similar to that of the species called *Drepanotrema* (*Fossulorbis*) *cultratum* (d'Orb.) in Baker's monograph. The latter is neither a typical *Drepanotrema* nor an *Anisus* according to its anatomy. The most important comparative feature of the shell as far as phylogeny is concerned is the development and direction of the spire. Nevertheless, in the genus *Helisoma* the sinistral, the discoidal and the pseudodextral shell types are present. Even within one species there can be both distinctly spired, sinistral forms and discoidal forms. In Planorbidae in general, however, the evolution of the shell form shows a decided trend, which will be more closely dealt with in the phylogenetical discussion.

External features not reflected by the shell, such as pigmentation, shape of head, tentacles, mantle border, mantle lobe, pseudobranch and foot, can sometimes be used as species characteristics. The differences in these features between groups are generally not significant. The mantle lobe and the pseudobranch show, however, some important differences within the Planorbidae.

The form of the kidney and some other pallial organs is strongly influenced by the degree of retraction of the animal at the moment of fixing. The details of the form and size of the kidney are, consequently, not reliable as taxonomic characters. The development of the ureter and its principal form is aberrant in some groups. The presence or absence of a muscle along the ventral surface of the kidney is a distinct feature. Three different types of ridges in the pallial cavity occur in Planorbidae. The renal ridge runs along the ventral surface of the kidney, the dorsal ridge runs behind the kidney and largely parallel to the caudal border of the latter, and lastly the rectal ridge is found along the dorsal

side of the rectum. This rectal ridge often continues outwards on the pseudo-branch. One or more of the ridges can be absent. Such differences are distinct and may be important. There can, however, be a considerable amount of intra-generic variation in such a feature (e.g. in *Amerianna*) and even intra-specific. In the species generally called "*Australorbis glabratus* (Say)" all stages from a well developed renal ridge to none at all can be observed. This vast range of variation seems, however, to be an exceptional rather than a common occurrence in planorbids. The rectal ridge is sometimes convoluted, forming an accessory gill.

In the digestive system differences occur in the form of the gizzard and in the form and position of the intestine. These features are not very distinct and cannot be favourably regarded as taxonomic characters. The morphology of the salivary glands is fairly uniform within the Planorbidae, but aberrant forms occur. The jaw and the radula are structures belonging to the digestive system that are morphologically more distinct. The jaw can be more or less well developed. Its lateral portions can be absent or at least non-chitinized. The jaw is generally almost homogeneous in structure, composed of a mass of hairlike chitinous formations, but sometimes it is built up of a comparatively small number of vertical plates. Sometimes only the dorsal portion of the jaw is composed of plates.

The only structure apart from the shell which has commonly been used for classification is the radula. This organ undoubtedly offers certain advantages but its value as a taxonomic character has been overestimated. The individual radula offers plenty of distinct details, though observational errors are sometimes easily made because of the small size of the organ. In the frontal part of the radula the teeth are generally worn and do not characterize their morphology in the species. But more important is the variability of the radula. Beside the fairly common irregularities in the formation of the teeth, there is a certain range of variation in the species. Occasionally, but not very often, the radula gives reliable characters to a species. More often, but not invariably, it gives characteristics for genera. The radula in general, however, can provide important taxonomic characters for groups of higher systematic rank.

In some animals, e.g. certain insects, the copulatory organs are considered so species-specific, cross-copulations of different species being prevented on purely mechanical grounds. This does not appear to be true in the Planorbidae, for copulation between different species has been observed. Physiological and cytogenetic differences between the species are rather decisive. There is, however, considerable morphological variation in the copulatory organs within the Planorbidae. In particular the male copulatory organ shows several different types and some peculiar specializations within the group. Some trends in the evolution of the male copulatory organ can be traced, and this structure gives more information than any other regarding relationships and phylogeny in Planorbidae. It is therefore important that it should be studied carefully, not only by dissection, as it was by Baker, but also by serial sectioning. It should also be noted that the male copulatory organ shows intra-specific variation which has to be considered when using the characters of the organ for comparative purposes. It is, for instance, worthless to make measurements of its different parts and then to base

comparisons on details of proportion. In addition to the ordinary genotypical variation there are considerable growth changes and seasonal changes in the male organ. The degree of contraction in the fixed organ affects its topographical morphology to a considerable extent.

Other structures of the genitalia, such as vas deferens, vagina and spermathecal system vary between species, and are more useful as species-discriminating characters than for characterizing genera. The prostate, on the other hand, can be used for classification within the family. The ovotestis, the seminal vesicle and the various glands are more liable to developmental changes than are the distal genitalia and they are, consequently, less useful for classification.

The nervous system is generally very reliable for comparative studies. Within the Planorbidae there are, however, but slight differences in the degree of concentration of the central nervous system. The peripheral nerves can be useful as means of identification when homologizing structures. Material fixed and preserved well enough for such studies has, unfortunately, been available for a few groups only.

To sum up, the male copulatory organ and the radula are the most important structures for phylogenetical studies in the Planorbidae. The prostrate is next in importance. Occasionally the pallial ridges, the jaw, the general shape of the shell, the central nervous system and the lateral appendages are important as characters for comparative studies. More rarely other features not mentioned above may also be used.

MORPHOLOGICAL CHARACTERISTICS OF REPRESENTATIVES OF THE PLANORBID GROUPS.

It is not my intention to give a complete account of the morphology of the different planorbids. Baker (1945) has already presented a comprehensive monograph on this subject. Nevertheless his material is incomplete and he has accounted neither for *Plesiophysa* and members of the Bulininae (with the exception of *Indoplanorbis*) nor for members of the Planorbinae with a *Physa*-like shell as well as some other groups. Further, certain morphological elements are too superficially dealt with by Baker and by authors in general. This is particularly true as far as the male copulatory system is concerned. For this reason I have laid stress on the internal structure of the male copulatory system. On the other hand, I have restricted my account mainly to characters of comparative value, i.e. characters of importance as a basis for classification and phylogenetic discussion. These characters have been discussed in the preceding section.

As Baker has a tendency to split taxonomic units, I consider it enough to use the recent genera accepted by him as a starting point. In addition I deal with the groups mentioned above not included by Baker in his monograph. For each group I have selected at least one species, preferably the type species, for morphological examination and description. For four genera I have not been able to obtain satisfactory material.

The groups described herein are alphabetically arranged, this being the most practical arrangement for the reader, who needs to compare the morphological descriptions when he is studying the phylogenetic discussion. For the various groups the morphological characters are given in the following order as far as

applicable: Shell and general form, lateral appendages, mantle organs, jaw, salivary glands, radula, male copulatory organ and prostate. Additional facts and remarks are given for some genera.

Acrorbis Odhner, 1937.

Material. *A. petricola* Odhner (the type species) from Nova Teutonia, State of Santa Catharina, Brazil. (Coll. H. Schade, 21 Aug. 1937; Riksmuseum, Stockholm.)

Morphology. The shell is decidedly pseudo-dextral.

The mantle lobe varies in size and can sometimes be extraordinarily well developed (fig. 1). The pseudobranch is also well developed but does not show any convolutions. The anal pore may be located almost between the two structures or in the ventral side of the pseudobranch. There is no renal ridge, dorsal ridge or rectal ridge. The urethra is straight, not reflected. The tiny, arch-formed jaw seems to lack the slender, lateral portions composed of vertical bars. It is doubtful whether the salivary glands are joined or not. The bicuspid centrals of the radula seem to be slightly asymmetrical (fig. 178 t). The first laterals are tricuspid with extraordinarily long, slender cusps. The marginals are broad with a set of caudal cusps. Though they are very short along their longitudinal axis, they certainly belong to the square-formed or short type of marginals. The radula sack is unusually long.

In the male copulatory organ the penis sheath is comparatively short (fig. 2). The penis is long and slender with a terminal pore (fig. 4). It has a dense tissue structure and a remarkably excentric lumen. No velum has been observed in the specimens examined. The praeputium does not show any peculiarities. There are two flagella composed of a single layer of about cube-shaped cells which give the impression of having a glandular function. There is, however, no connection between the lumen of the flagella and the penis sheath.

The prostate is composed of a number of finger-shaped or slightly club-shaped diverticular protruding in different directions from vas deferens (fig. 3).

Remarks. Odhner (1937) considers *Acrorbis* related to *Pompholycodea* (= *Parapholyx*). There is a certain conchological similarity between the two groups but most anatomical characteristics contradict this supposed relationship. Odhner says: "durch die Radula und den Kiefer erweist sich aber *Acrorbis* primitiver, da diese mehr vom Planorbistypus sind, bei *Pompholycodea* aber etwas spezialisiert erscheinen". Actually, however, *Acrorbis* has the more specialized and *Parapholyx* the more primitive type of radula and jaw. The square-formed marginals or marginals with only posterior cusps as well as vertical bars in the jaw are certainly new developments within Planorbidae. Further, a relationship between *Acrorbis* and *Parapholyx* is contradicted firstly by important differences in the male copulatory organ and secondarily also by differences in the prostate, the mantle organs and the mantle opening appendages.

Baker (1945) concludes that *Acrorbis* is related to *Drepanotrema*, though distinct by both shell and anatomy. He based this conclusion on the general form of the prostate and other structures in the genitalia. He supposed that the apparent differences in the radula are due to observational errors. Though not very detailed, Odhner's description and figure of the radula in *Acrorbis* is not incorrect.

Figs. 1-4.

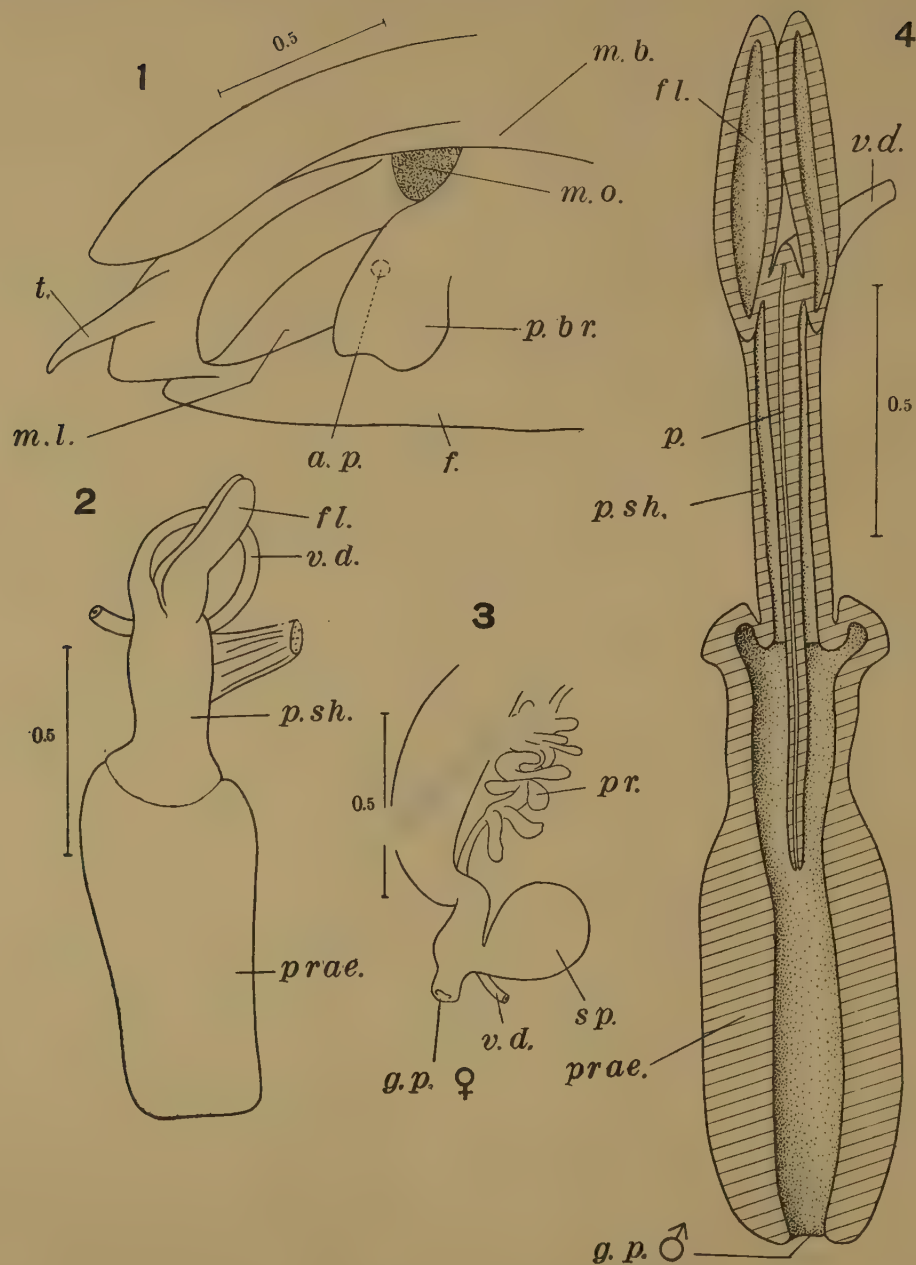
*Acrorhis petricola* Odhner.

Fig. 1.—Frontal portion of left side of animal.

Fig. 2.—Male copulatory organ.

Fig. 3.—Female copulatory organ and prostate.

Fig. 4.—Longitudinally sectioned male copulatory organ.

(In all figures the hatched areas indicate cut surfaces. Unless otherwise indicated the scale alongside each figure is 1 mm.)

(Key to lettering, p. 542)

Afroplanorbis Thiele, 1931.

Material. *A. pfeifferi* (Krauss) from Salisbury, S. Rhodesia. (Coll. W. Alves, Aug. 1952; collection of G. Mandahl-Barth, Copenhagen.)

Morphology. The shell has a simple discoidal form.

The mantle lobe (fig. 5) is of moderate size but formed as a distinct furrow or rather an incomplete funnel. The pseudobranch is well developed. The rectal

Figs. 5-8.

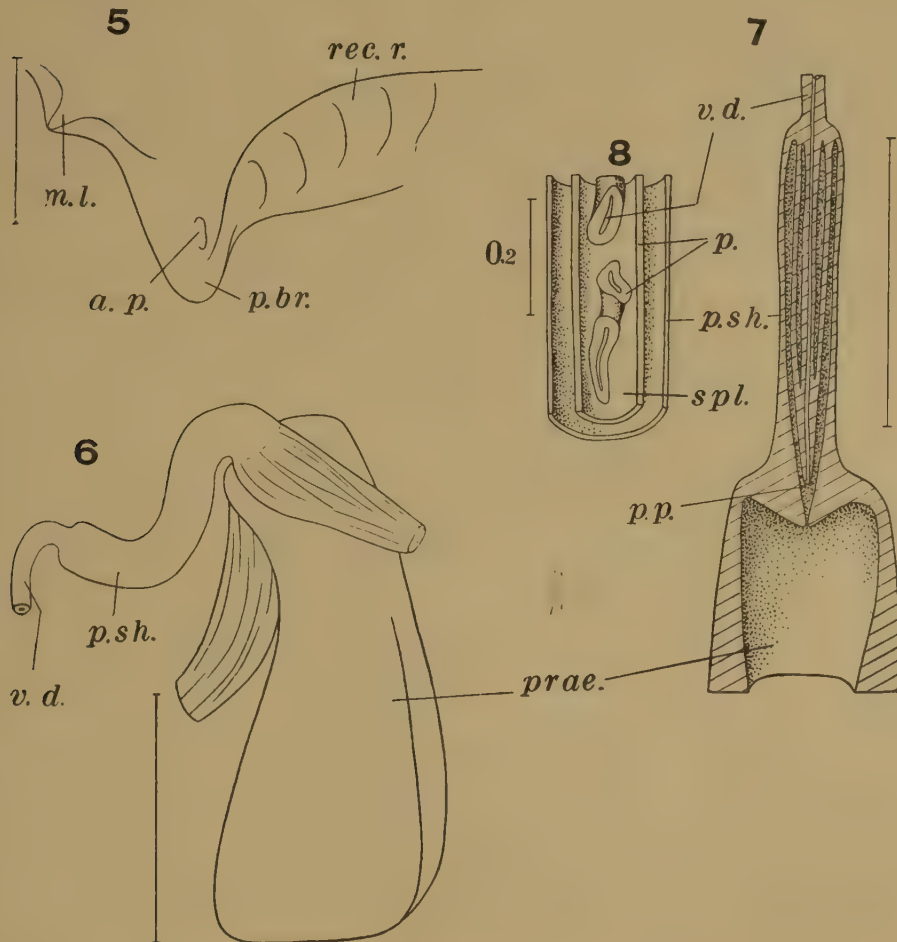
*Afroplanorbis pfeifferi* Krauss.

Fig. 5.—Mantle lobe, pseudobranch and distal portion of rectal ridge seen from left side.

Fig. 6.—Male copulatory organ.

Fig. 7.—Longitudinally sectioned proximal portions of male copulatory organ.

Fig. 8.—Part of the penis sheath and penis as in fig. 7.

(Key to lettering, p. 542)

ridge begins on it and the anal pore is situated dorsally in front of the rectal ridge. No renal ridge is present in the mantle cavity. A dorsal ridge and, as already noted, a rectal ridge occur. The latter has well-developed transverse folds containing blood vessels. The jaw has no vertical bars and its lateral parts are weak. The salivary glands are lobed and fused posteriorly.

The centrals and laterals of the radula (fig. 177 *k*) are of the ordinary Planorbis type. The marginals are of the long type with cusps directed postero-laterally.

In the male copulatory organ (figs. 6–8) the praeputium is strongly predominating. The penis has a terminal pore. The vas deferens with some surrounding tissue runs in a sinus inside the peripheral tissue of the penis. The praeputium does not show any special features.

The prostate is composed of a number of diverticula from the vas deferens. All except the first or most distal one are branched. The number of main diverticulae is about thirteen.

Remarks. Baker did not examine any material of this group but he quoted some notes from Pilsbry (1934) and Watson (1925). These authors have found the prostate to consist of five main branches, each of which branches again two or four times. Ranson & Cherbonnier (1952 *a, b*) have figured the prostate in a similar way. They have studied also a few other species of *Afroplanorbis*, i.e. *A. adonensis* (Bourguignat) and the type species *A. sudanicus* (v. Martens). In all these species the prostate shows the same general pattern though the number of diverticula and their degree of branching varies. In none of the species do the prostate diverticula branch off from a separate prostatic duct as Baker says.

Baker rightly mentions the similarity between *Afroplanorbis* and *Tropicorbis*.

Amerianna Strand, 1928.

Material. *A. leopoldi* (Dupuis) from Angi-Gita Lake, Arfak, New Guinea. (Coll. 9 March 1929; Inst. Roy. Sci. nat. Belg., Brussels.)—*A. buruanus* (Bentham-Jutting) from Rana-Lake, Buru Island. (Coll. by L. J. Toxopeus 1921; Zool. Mus. Amsterdam)—*A. pesigani* Hubendick from Tibok River, Ortega, 7 km. West of Palo, Leyte and from Borbocolon, 30 km. South of Calapan, Mindoro in the Philippines. (Coll. by B. Hubendick, 7 July and 7 August 1952 respectively.)—*A. obesa* Adams from Somerset Dam, S.E. Queensland. (Coll. by I. D. Hiscock, 18 Feb. 1953.)

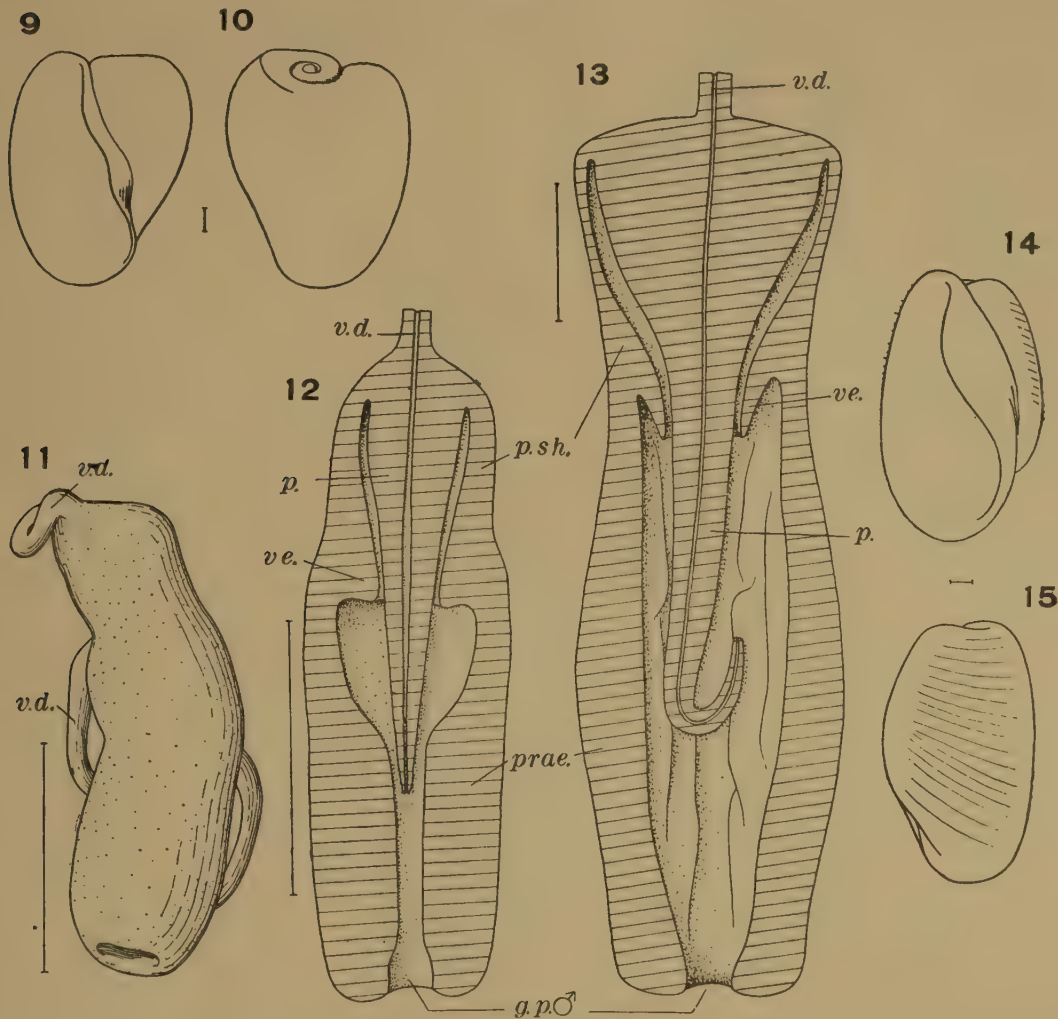
Morphology. The shell is sinistrous with a well-developed spire (fig. 20) or a very reduced spire (figs. 9–10). In *A. leopoldi* (figs. 14–19) the spire is completely surrounded by the body whorl. In *A. obesa* the tentacles are very short.

The mantle lobe (fig. 19) is furrow-shaped and the anal pore is situated caudally on its ventral surface. The pseudobranch is very well developed. The caudal flap of the mantle lobe continues across the pseudobranch. The latter is richly folded dorsally and ventrally to this flap. In *A. leopoldi* this division of the pseudobranch into a dorsal and ventral part does not occur. The conditions in the mantle cavity are different in the various species. In *A. buruanus* and *pesigani* the ureter is reflected but in *A. leopoldi* and *obesa* it is S-shaped. A short renal ridge occurs in *A. buruanus*. A short dorsal ridge is present in *buruanus*, *pesigani* and *obesa*, a very thin rectal ridge in *pesigani* and a stouter one in *buruanus*. In *obesa* there are two rectal ridges. In *A. leopoldi* no ridges were observed. The jaw has vertical bars. The lobed salivary glands are fused posteriorly.

The centrals and laterals of the radula (fig. 177 *e*) are of the ordinary planorbis type. The marginals are of the long type. In *A. leopoldi* there is a number of caudal cusps and one lateral cusp.

The male copulatory organ is simple in *Amerianna* (figs. 11-13, 17-18). There is a comparatively short penis sheath which is not very distinctly set off from the praeputium. The penis has a terminal (in *A. pesigani* it is almost terminal) pore,

Figs. 9-15.

*Amerianna*

Figs. 9-12.—*Amerianna buruanus* (Bentham-Jutting).

Figs. 9-10.—The shell, ventral and dorsal view respectively.

Fig. 11.—Male copulatory organ.

Fig. 12.—Longitudinally sectioned male copulatory organ.

Figs. 13-15.—*Amerianna leopoldi* (Dupuis).

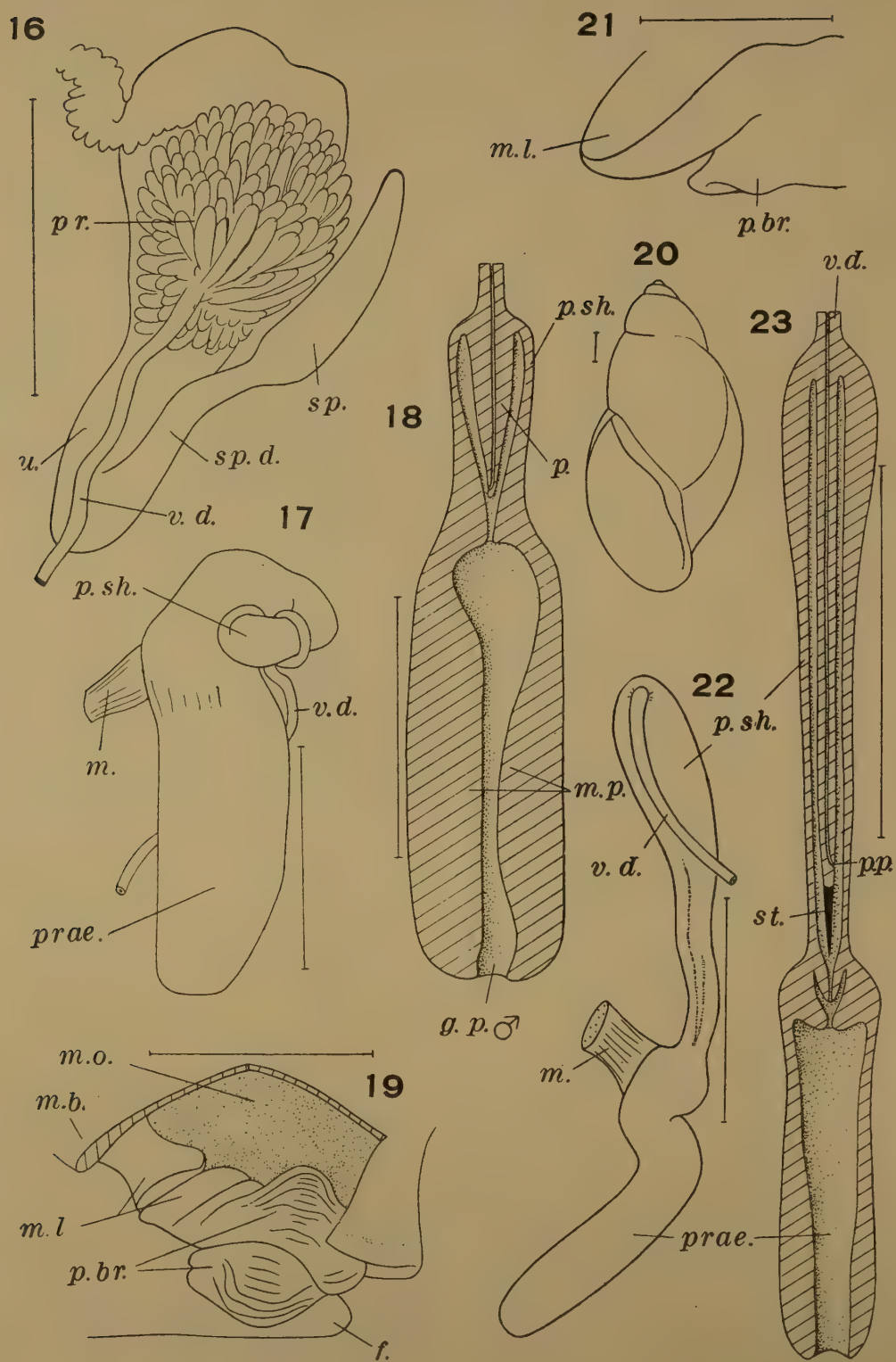
Fig. 13.—Longitudinally sectioned male copulatory organ.

Figs. 14-15.—The shell. Ventral and dorsal view respectively.

(Key to lettering, p. 542)

but the form of the penis varies. In *A. pesigani* it is circular in cross-section, in *buruanus* irregularly rectangular, in *leopoldi* triangular and, further, in *obesa* rounded with a tendency to be triangular in cross-section.

Figs. 16-23.



The prostate is composed of a large number of diverticula from the vas deferens (fig. 16).

In all four species the spermatheca is more or less long and slender (fig. 16).

Anisus Studer, 1820.

Material. *A. vortex* (L.) from the mouth of Hjälmare Kanal into Lake Hjälmare, Södermanland, Sweden. (Coll. B. Hubendick, 21 June 1945; Uppsala Univ. Mus.)

Morphology. The shell is flat with many whorls, very slowly increasing in diameter. All whorls are visible on both sides. Small aperture.

The mantle lobe (fig. 21) is of ordinary size and furrow-shaped. The pseudo-branch is small and without folds but with almost terminal anal pore. In the mantle cavity neither renal ridge, dorsal ridge nor rectal ridge is present. The jaw has vertical bars.

The centrals and laterals of the radula (fig. 178 k) are of the ordinary form in Planorbidae. The marginals are of the square type without lateral cusps.

In the male copulatory organ (figs. 22–23) the penis sheath is considerably longer than the praeputium. The proximal portion of the former has a thick wall consisting of regularly arranged oblique radial and longitudinal muscles. The penis forms a compact tissue structure surrounding the vas deferens which opens laterally not far from the terminal, cuticular stilett. The sarcobelum contains some circular muscles and comparatively compact connective tissue and the velum has regularly arranged radial muscles. No special structures occur in the praeputium. The muscular pillars are weakly developed.

The prostate has a number of unbranched diverticula from a separate prostate duct.

Through the courtesy of Dr. L. L. Forcart (Naturhist. Museum, Basel) paratypes of *Anisus sarasinorum* Bollinger from Lake Lindu, Central Celebes, have been available for this investigation. Though this species is more closely related to *Anisus* than to any other already defined genus, it shows some differences from other species of *Anisus*. The most important difference is a big gland in the proximal portion of the praeputium (fig. 173). The size of the gland results in a projecting bulb on the outside of the praeputium (fig. 172). There are no muscular pillars. In the lower end of the penis sheath there is a well-developed layer of radial muscles outside the circular muscle layer. The prostate has one

Figs. 16–20.—*Amerianna pesignani* Hubendick.

Fig. 16.—Female copulatory system and prostate.

Fig. 17.—Male copulatory organ.

Fig. 18.—Longitudinally sectioned male copulatory organ.

Fig. 19.—Mantle pore region seen from the left. Part of the mantle cut away.

Fig. 20.—The shell.

Figs. 21–23.—*Anisus vortex* (Linné).

Fig. 21.—Mantle opening appendages seen from left and behind.

Fig. 22.—Male copulatory organ.

Fig. 23.—Longitudinally sectioned male copulatory organ.

(Key to lettering, p. 542)

row of diverticula arising from a prostatic duct. The diverticula give off one or possibly two branches on the medial side.

Remarks. Buchner (1891) had already discovered the main features of the male copulatory organ. Baker (1945) examined *A. vortex* (L.), *spirorbis* (L.), *septemgyratus* (Ziegler) and *leucostomus* (Millet). The latter, however, is probably identical with *A. spirorbis* (cf. Hubendick, 1951). The former's results show that the anatomy of the European species of *Anisus* is fairly uniform though some features, not accounted for above, vary to a considerable extent. However, the anatomy of the East Indian species *sarasinorum* shows that the group is more heterogenous than the European species indicate.

Armiger Hartmann, 1840.

Material. *A. crista* (L.) (the type species) from a stream to Lake Yngaren at Björkvik, Södermanland, Sweden. (Coll. B. Hubendick, 7 Aug. 1944; Uppsala Univ. Mus.)

Morphology. The shell is slightly pseudo-dextral.

The mantle lobe (fig. 24) is of the usual size and is furrow-shaped. The pseudo-branch is almost non-existent. There is no renal ridge, dorsal ridge or rectal ridge. The jaw has vertical bars.

The centrals and laterals of the radula (fig. 178 m) are of the ordinary planorbid type. The marginals are square-formed and lack lateral cusps.

In the male copulatory organ (figs. 25–26) the penis sheath and the praeputium are separated by a sarcobelum and a velum. The penis wears a very tiny terminal stiletto and the vas deferens opens laterally some distance above the stiletto. The whole organ is similar to that of *Anisus* but the proximal portion of the penis sheath does not show any special arrangement of the musculature.

The prostate consists of a number of simple diverticula from a separate prostatic duct.

Remarks. The anatomy of *Armiger crista* has been studied by Odhner (1929), Soós (1935) and Baker (1945). In all these investigations the stylet has been overlooked. The supposed absence of a stylet has encouraged the respective authors to keep *Armiger* generically distinct from *Gyraulus*.

Australorbis Pilsbry, 1934.

Material. *Australorbis glabratus* Say (the type species). Extensive material from different localities in Venezuela collected by the author in Feb.–April 1953.

Morphology. The shell has a simple discoidal form.

The mantle lobe is formed as an incomplete funnel. The pseudobranch is well developed. The rectal ridge begins almost terminally on it. The anal pore is situated anteriorly to the rectal ridge. The latter has big transversal folds containing blood vessels so that the rectal ridge is probably working as an accessory gill. A very blunt, fleshy renal fold is present. It is not similar to the thin and slender renal fold in some other groups. In some very similar, obviously closely related forms the renal fold is entirely lacking. A dorsal fold is present. The jaw has no vertical bars.

Figs. 24-31.

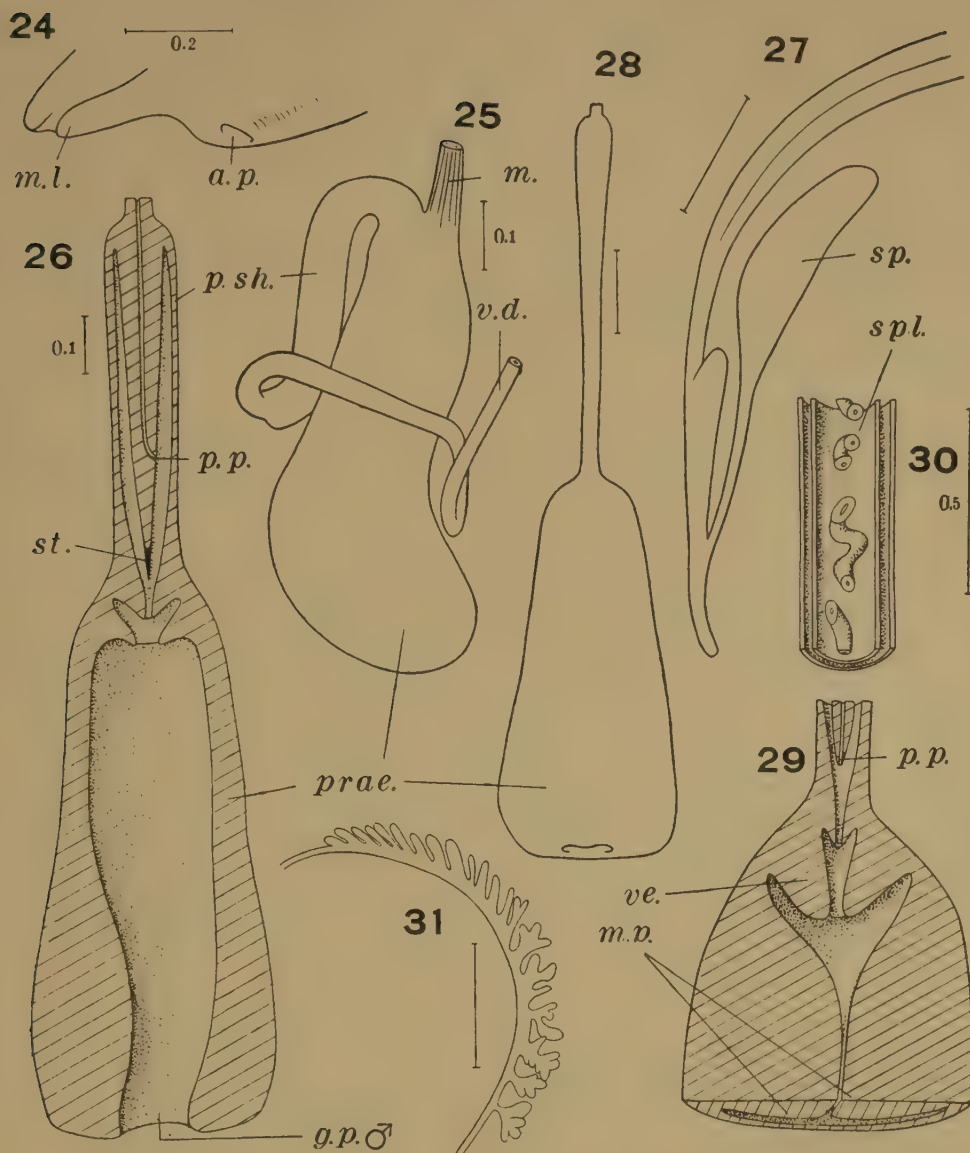
Figs. 24-26.—*Armiger crista* (Linné).

Fig. 24.—Mantle opening appendages. Seen from the left.

Fig. 25.—Male copulatory organ.

Fig. 26.—Longitudinally sectioned male copulatory organ.

Figs. 27-31.—*Australorbis glabratus* (Say).

Fig. 27.—Female copulatory system.

Fig. 28.—Male copulatory organ.

Fig. 29.—Longitudinally sectioned middle portion of male copulatory organ.

Fig. 30.—Longitudinally sectioned portion of penis and penis sheath.

Fig. 31.—Prostate. Distal end turned down.

(Key to lettering, p. 542)

The centrals and laterals of the radula (fig. 177 *l*) are of ordinary Planorbidae type. The marginals are of the long type with caudal and lateral cusps.

In the male copulatory organ (figs. 28–30) the penis sheath is slender and the praeputium is thick. The muscular pillars in the latter are well developed. The penis has a terminal pore and a voluminous sinus surrounding the central, somewhat coiled portion of the penis with the vas deferens. The prostate (fig. 31) has a number, generally about twenty, partly branched diverticula arising directly from the vas deferens.

The female duct has a small, blind-ending diverticulum within a short distance of the entrance of the spermathecal duct (fig. 27). This feature seems to be of specific rather than generic value because other, closely related species do not correspond to this pattern.

Biomphalaria Preston, 1910.

Material. *B. smithi* Preston (the type species) from Vitshumbi, Lake Edward, Uganda. (Coll. Dr. Wanson, 21 Sept. 1949; collection of G. Mandahl-Barth, Copenhagen.)

Morphology. The shell is discoidal with the last portion of the whorl somewhat depressed, giving the shell a slight trace of pseudo-dextrality.

The mantle lobe (fig. 32) is formed as an incomplete funnel. The pseudobranch is well developed with an almost terminal anal pore. The well-developed, folded and richly vascularized rectal fold begins on the pseudobranch. There is no renal ridge but there is a dorsal one. The jaw has no vertical bars, its lateral parts are weak. Salivary glands long, lobated and fused posteriorly.

The centrals and laterals of the radula (fig. 177 *i*) are of the ordinary type in the Planorbidae. The marginals are long and have cusps also along the lateral edge.

The male copulatory organ (figs. 33–34) has a slender penis sheath. The penis has a terminal pore and a wide sinus around the vas deferens and surrounding tissue. The praeputium is big and has well-developed muscular pillars in its distal half.

The prostate (fig. 35) has several diverticula branched just close to their base. They are situated on the vas deferens, not on a separate prostate duct. Ranson & Cherbonnier have studied *B. smithi* and *B. choanomphalus* v. Martens (1952 *b*) as well as *B. rüppellii* (Dunker) (1952 *a*). According to them the two first-mentioned species have a comparatively limited number of diverticula, which are branched distally only but have broad bases. This difference may indicate a considerable intrageneric and intraspecific variation. Another possible explanation is that the prostate of the specimens examined by Ranson & Cherbonnier were not full-grown. In *B. rüppellii* their figure shows a number of club-shaped diverticula more or less branched distally. In all species mentioned here the prostatic diverticula are not situated on a special duct but are on the vas deferens.

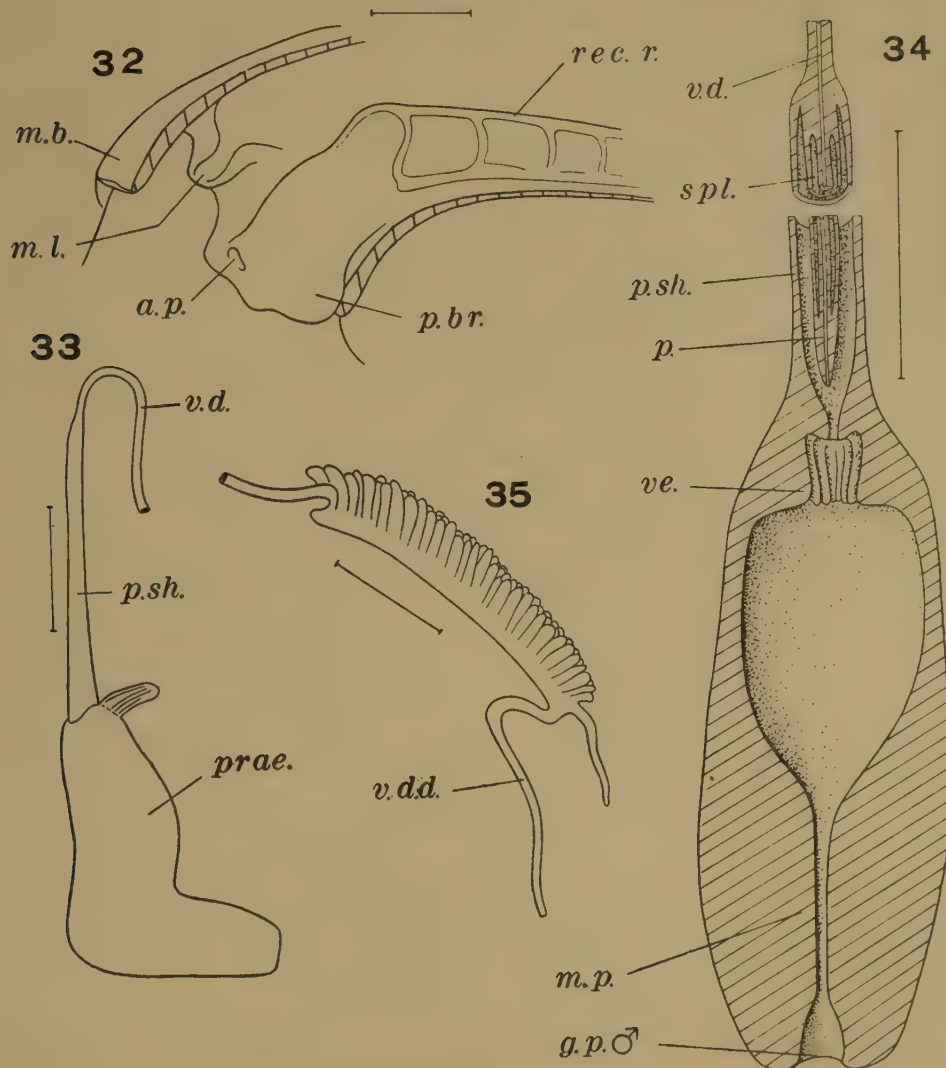
Bulinus Müller, 1781.

Material. In addition to the material accounted for under *B. natalensis* (Küster), *B. tropicus* (Krauss), *B. inflatus* (Adams & Adams), *B. newcombi* (Adams & Angas)

and *B. senegalensis* Müller (=type species) in my earlier paper (1948 a) some new specimens of African *Bulinus* have come to hand.

Morphology. Sinistral shell with a distinct spire. Smoothly rounded aperture. Umbilicus present.

Figs. 32-35.



Biomphalaria smithi Preston.

Fig. 32.—Mantle opening region seen from left side. Part of the mantle cut away.

Fig. 33.—Male copulatory organ.

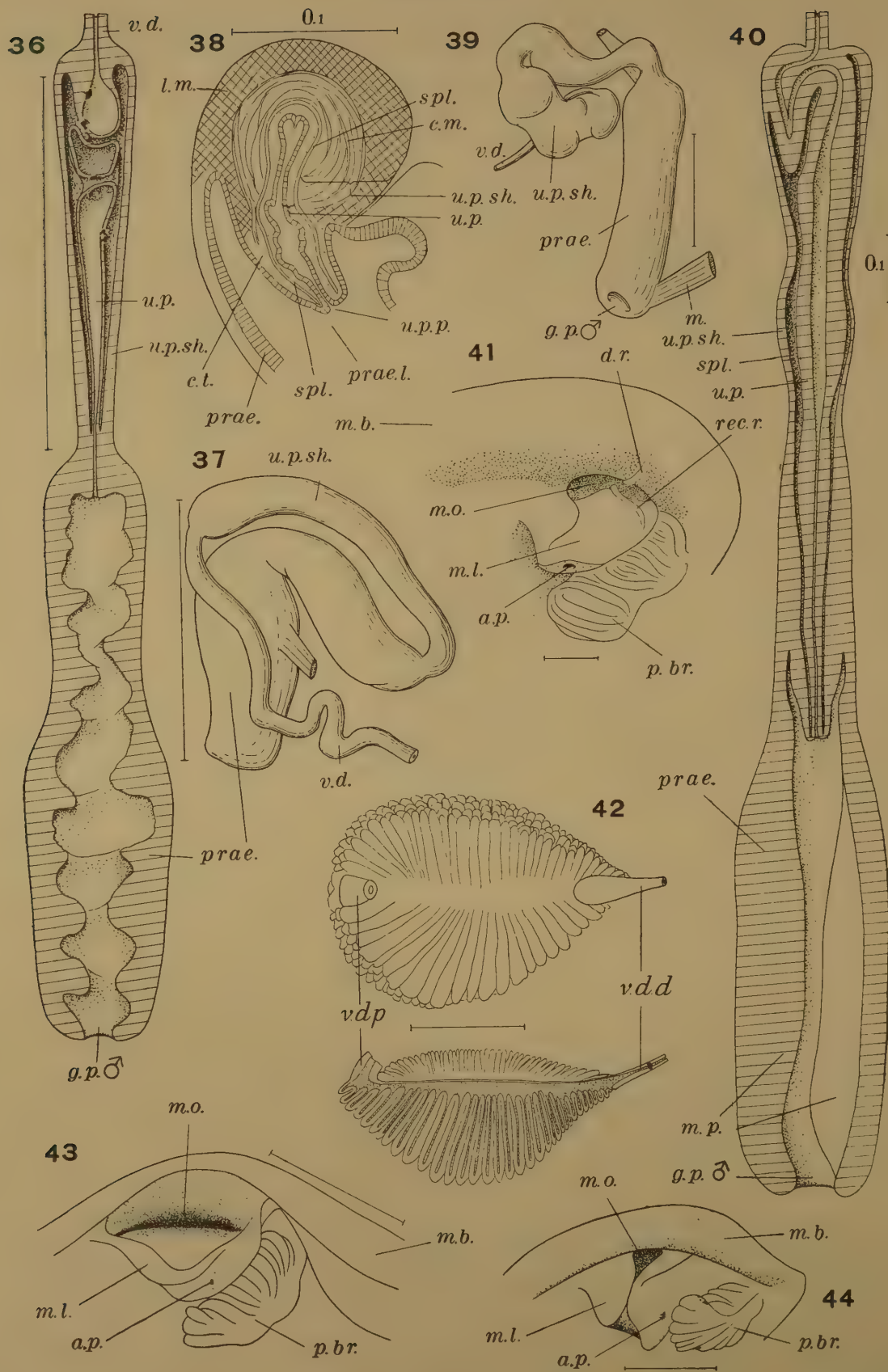
Fig. 34.—Longitudinally sectioned male copulatory organ. The middle portion of penis and penis sheath are left out.

Fig. 35.—Prostate. Distal end turned down.

(Key to lettering, p. 542)

The mantle lobe (figs. 41, 43-44) is well developed. According to its position at the moment of fixation it may be formed as an almost complete funnel with a narrow slit dorsally only, an open, almost flat furrow-like flap or anything between

Figs. 36-44.



these extremes. The anal pore opens ventro-posteriorly on the lobe. The rectal ridge is continued out on the dorso-posterior surface of the lobe. Its posterior portion often covers the anterior part of the pseudobranch. This is big and very richly folded. Both rectal and dorsal folds are always present. A short renal fold occurs along the distal portion of the kidney in the Australian *B. inflatus* but it is totally lacking in the African forms. The jaw is comparatively weak and has no vertical bars. The salivary glands are sausage-shaped and connected posteriorly.

The radula is of the ordinary planorbid type (fig. 177 c). The marginals are of the long type with at least a tendency to form lateral cups in addition to the caudal ones.

The male copulatory organ (figs. 36–40) differs principally from that of other planorbids and basommatophores in general. There is no pendant penis of the ordinary type in *Bulinus* but what has been called pseudo-penis (Hubendick, 1948 a). At a malacological meeting in Paris 1954, it was agreed that the structure should be called ultra-penis. The praeputium, on the contrary, is of the ordinary type. The ultra-penis consists of some tissues which are separated from the pseudo-penis sheath by an extensive sinus. It is connected with the ultra-penis wall at its proximal end where the vas deferens enters and at the junction between the ultra-penis sheath and the praeputium. The organ is more closely dealt with under the genus *Physopsis*. The structure is completely similar in the two groups.

The prostate (fig. 42), which is described by Hubendick (1948 b), consists of a great number of unbranched diverticula from the vas deferens. The organ is almost hemispherical.

Camptoceras Benson, 1843.

Material. *C. hirasei* Walker from Lake Biwa, Shiga Prefecture, Japan. (Coll. T. Habe, 4 June 1954.)

Morphology. The shell is sinistral with a high spire. Most of the shell material seems to consist of periostracum.

Outside the mantle opening there is one wide flap (fig. 45). The anal pore is on a bulb in the middle of the base of this flap. There is, consequently, no separate mantle lobe or pseudobranch. A comparatively low and rounded rectal

Bulinus.

Fig. 36.—*B. senegalensis* Müller. Longitudinally sectioned male copulatory organ.

Fig. 37.—Same species. Male copulatory organ.

Fig. 38.—*B. natalensis* (Küster). Section through the connection between ultra-penis, ultra-penis sheath and praeputium. The upper portion is transversally, the lower portion longitudinally sectioned due to the organ being curved.

Fig. 39.—*B. tropicus* (Krauss). Male copulatory organ.

Fig. 40.—*B. natalensis*. Longitudinally sectioned male copulatory organ.

Fig. 41.—*B. inflatus* (Adams & Angas). Mantle opening region seen from the left.

Fig. 42.—Same species. Total view of the prostate (above) and longitudinally sectioned prostate below.

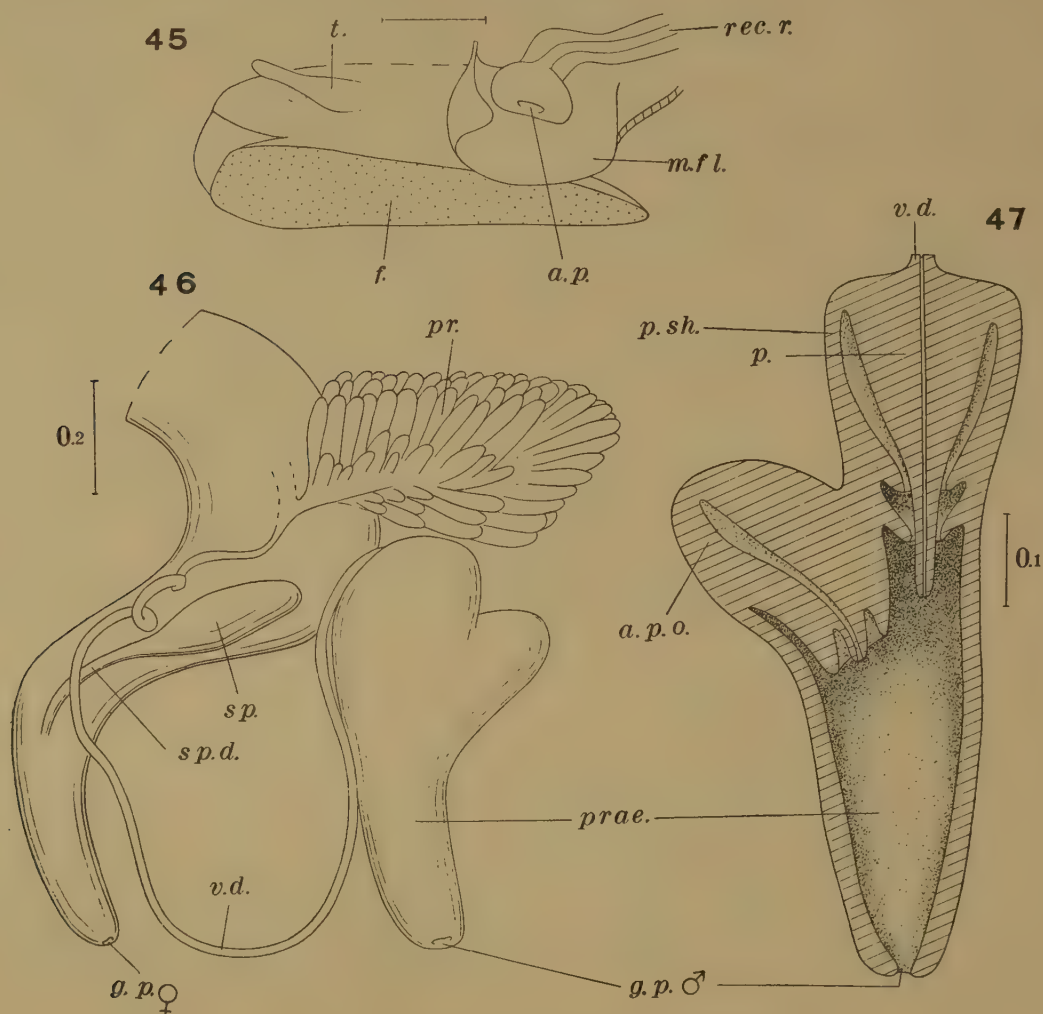
Fig. 43.—*B. tropicus*. Mantle opening region seen from the left.

Fig. 44.—*B. natalensis*. Mantle opening region seen from the left.

(Key to lettering, p. 542)

ridge and a similar dorsal ridge are present. Both run in an almost longitudinal direction. There is no renal ridge. The kidney has an S-shaped urethra. The jaw has no vertical bars. The salivary glands are globose; a junction between them posteriorly has not been observed.

Figs. 45-47.



Camptoceras hirasei Walker.

Fig. 45.—Left side of ventral part of animal. Mantle border removed.

Fig. 46.—Distal parts of generative organs.

Fig. 47.—Longitudinally sectioned male copulatory organ.

(Key to lettering, p. 542)

The centrals of the radula (fig. 177 *h*) are quadricuspid, the lateral cusps being very small. The inner laterals have four cusps. The marginals are of the long type with a set of posterior and a set of lateral cusps, the two groups of cusps being separated by a space.

In the male copulatory organ (figs. 46-47) the penis sheath is broader than the praepitium. The latter has, however, a big projecting structure at its upper end.

This structure has a thick wall of muscular tissue. Centrally there is a lumen which opens into the main lumen of the praeputium through a small papilla surrounded by a velum-like fold formation. There are some crystalline bodies among the muscles of this, as it seems, accessory organ. The epithelium of its lumen consists of small cells. In the upper end of the lumen there appear to be some glandular cells in the epithelium. The tissue is not well-preserved enough to allow a definite conclusion. There are no muscular pillars in the praeputium. There are no sinuses in the penis. The vas deferens opens terminally on the penis.

The prostate (fig. 46) consists of a large number of tubules. It is not clear whether all the tubules arise direct from the vas deferens or whether there is a short prostatic duct.

Remarks. The morphology of *Camptoceras* has been studied by Annandale & Prashad (1919, 1920) and Walker (1919); their contributions have been examined critically by Hubendick (1955 *b*) who discussed the phylogenetic position of the group.

Carinifex Binney, 1863.

No spirit material of *Carinifex* has been available for this investigation. The following notes on the morphology of the genus have been extracted from Baker's monograph.

The shell is pseudo-dextral. The pseudobranch is like that in *Helisoma*. There is no renal ridge but dorsal and rectal ridges are present. The peculiar jaw is horseshoe-shaped and not divided into one dorsal and two lateral parts. The whole jaw is composed of many small, vertical plates, which, however, are not similar to the vertical bars found in various other groups. The marginals of the radula (fig. 178 *f*) are of the long type with cusps also along the lateral edge.

According to Baker's description and figures the male copulatory organ seems to be similar to that in *Helisoma*. The accessory praeputial organ (penial gland according to Baker) and the arrangement of the accessory duct within the organ are apparently of the same pattern as in *Helisoma*. The free portion of the accessory duct is, however, much shorter than in *Helisoma*. Two muscular pillars are present in the praeputium. Baker figures the penis pore as situated terminally on the penis. This is probably incorrect as *Helisoma* and other related genera have a lateral penis pore and as Baker states that the pore is terminal also in these genera. The prostate consists of a number of diverticula from the vas deferens, each diverticulum having two rows of lobes.

Choanomphalus Gerstfeldt, 1859.

Material. *C. amauronius* Bourguignat from River Murinka at Lake Baikal. (Coll. 20 June 1906; Riksmuseum, Stockholm.)

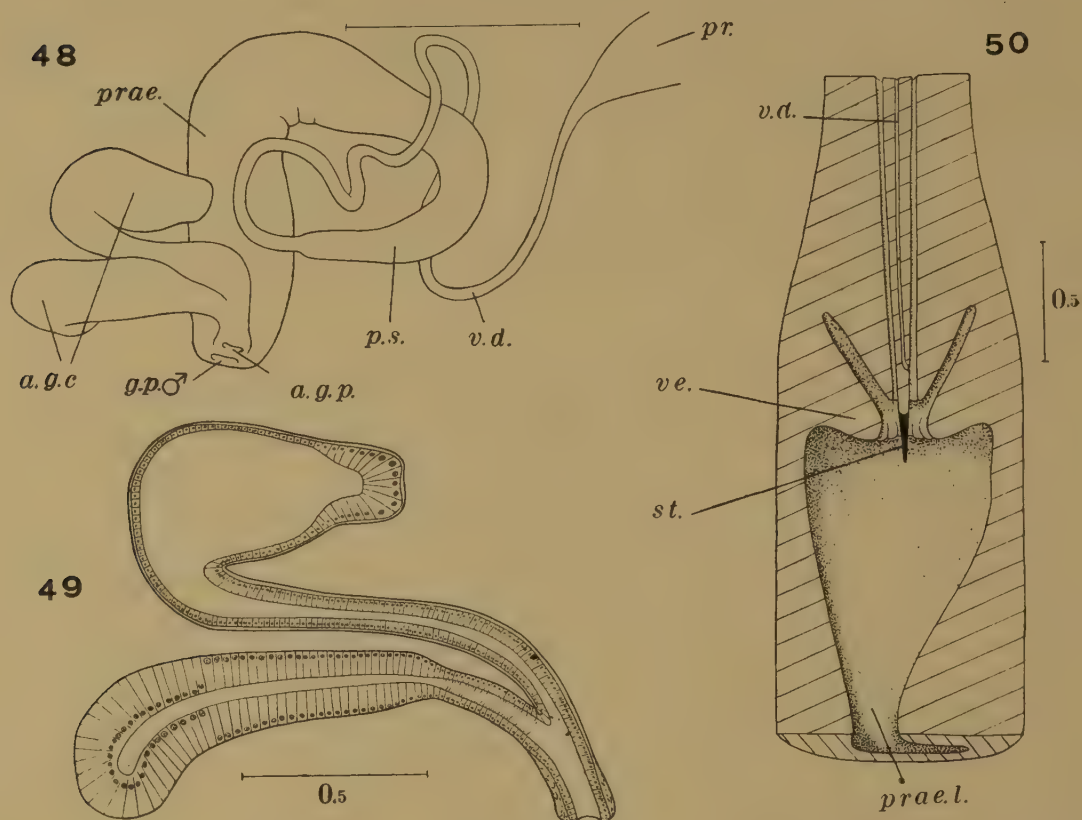
Morphology. A decided pseudo-dextral shell. The height of the spire and the size of the umbilicus, etc. are different in the various species. The shell is somewhat similar to that of *Valvata*.

Below the pallial opening, and below the portion posterior to it, is a well-developed flap. The anal pore is located on the posterior part of this flap. Neither renal

ridge, dorsal ridge nor rectal ridge occurs. The jaw has vertical bars. The salivary glands are sausage-shaped and connected posteriorly.

The radula (fig. 178 *h*) is mainly of the ordinary planorbid type. The epithems are unusually well developed. The marginals are square-shaped and without lateral cusps.

Figs. 48–50.



Choanomphalus amauronius Bourguignat.

Fig. 48.—Male copulatory system.

Fig. 49.—Semi-schematic diagram of longitudinal section through accessory gland complex.

Fig. 50.—Longitudinal section through lower portion of penis and penis sheath and upper portion of praeputium.

(Key to lettering, p. 542)

The male copulatory organ (fig. 48) has a distal accessory gland complex (fig. 49), and as far as known without any trace of an equivalent in any other planorbid group. The limit between the penis sheath and the praeputium is indistinct on the outside. The penis sheath has a thick wall and a narrow lumen almost entirely filled up by the penis (fig. 50). The peripheral wall of the penis has a flattened epithelium covered with a cuticula, and the bulk of the penis consists of a very dense tissue structure probably made up of radial and longitudinal muscles. The vas deferens opens laterally some distance proximally to the point of the penis, which, forming a stylet, is cuticularized throughout. There is a well-developed

sarcobelum and velum. There are two thickened portions along the praeputial wall, one of them being a well-developed muscular pillar.

The details of the prostate are unknown but the organ probably consists of a number of diverticula from the vas deferens.

Remarks. *Choanomphalus* is a somewhat aberrant planorbid not only as to its shell and general form but also in some other details. In the first place there is the above mentioned accessory gland complex. Other special features are the straight kidney, the big radula pocket, the unusually long epithem of the radula teeth and, probably, an extraordinarily concentrated nervous system (fig. 204). A full account of these details is given by Hubendick (1954).

Drepanotrema Fischer & Crosse, 1880.

Material. *D. anatinum* (d'Orbigny) (the type species) from five localities in Venezuela.—*D. lucidus* (Pfeiffer) from two localities in Venezuela.—*D. aeruginosus* (Morelet) from one locality in Venezuela. All the material was collected by the author during March and April 1953.

Morphology. Shell discoidal or slightly pseudo-dextral. The body whorl is dominating and in some species embraces the previous whorl. Left side or both with a central concavity. The shell form is very different in the various species and the extremes approach the shell forms of *Anisus contortus* (L.) and *Gyraulus riparius* (Westerlund).

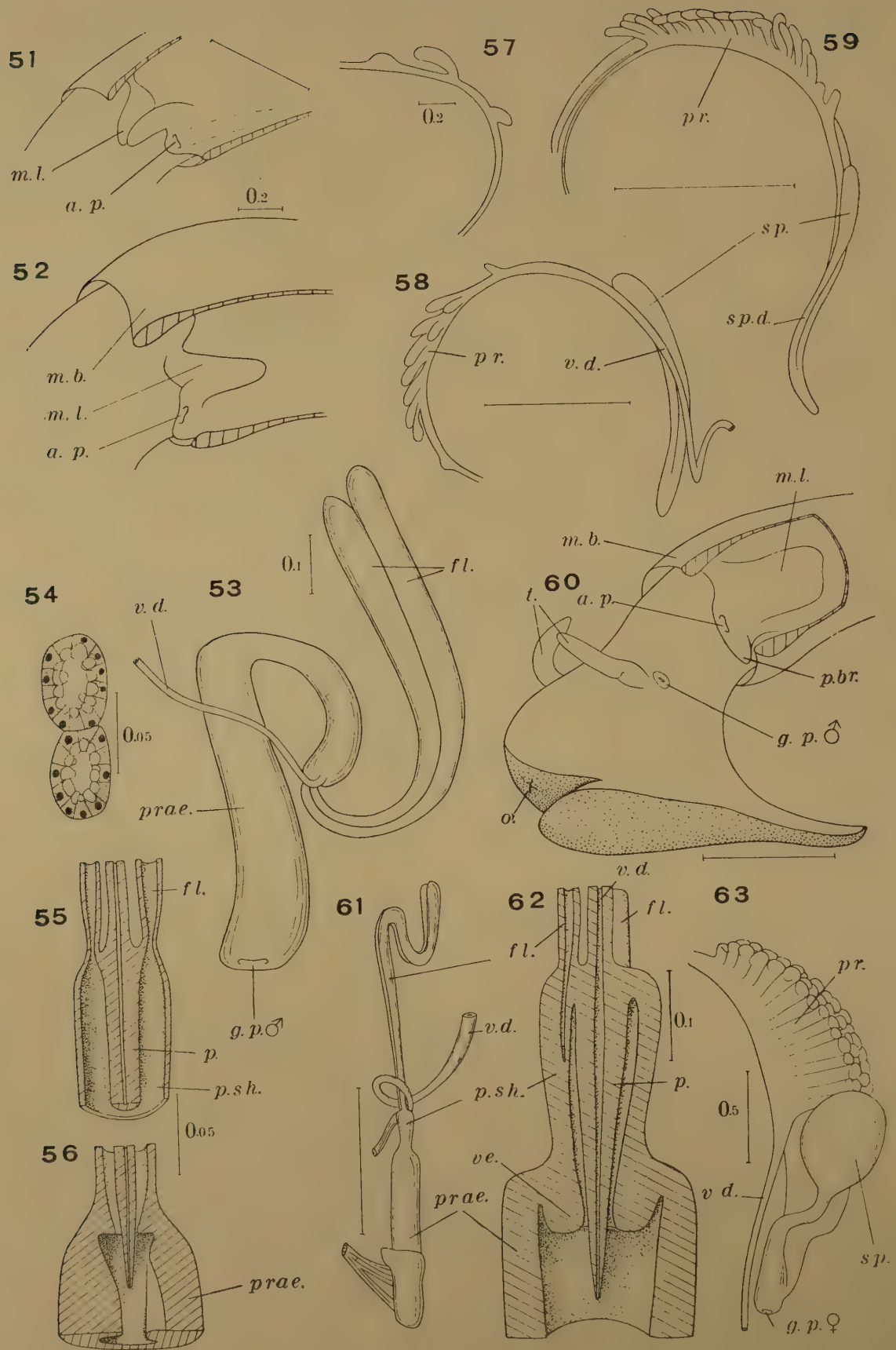
The mantle lobe (fig. 51) is comparatively small and formed as an open furrow. In some of the specimens examined part of the mantle lobe or the whole lobe is extended to form a thin flap which is turned into the mantle cavity (figs. 52, 60). Renal, dorsal and rectal ridges are lacking except in *D. aeruginosus* where a dorsal ridge and a very small rectal ridge are present. This species is aberrant also in other respects, e.g. in having a *Gyraulus*-like shell. The jaw is very weak. It consists of a number of more or less free pieces as in Ancyliidae. The salivary glands are sausage-shaped and connected posteriorly.

The radula (fig. 177 p) has long marginals with posterior and lateral cusps. Its centrals are peculiar through having one small lateral cusp on either side of the main cusps.

The male copulatory organ (figs. 53, 61) is characterized by two flagella. Baker (1945) says that in *D. anatinum* the one flagellum is bifid at the tip. The fact that there are two complete flagella was probably overlooked by Baker. In all specimens examined by me, except in the *Gyraulus*-like *D. aeruginosus*, the lumina of the flagella are connected with the lumen of the penis sheath. In the *D. aeruginosus* such a connection seems not to exist (fig. 62). Each flagellum is built up of a single layer of comparatively big glandular cells inside a very thin layer of connective tissue (fig. 54). The penis has a terminal pore. There is a poorly developed sarcobelum but no velum. In the praeputium there are two muscular pillars.

The prostate in *D. anatinum* (fig. 58) consists of ten, somewhat irregularly arranged, diverticula arising from the vas deferens; according to Baker seven diverticula only are present. Sometimes the number of diverticula is still smaller

Figs. 51-63.



and they are widely interspaced (fig. 57). In the two remaining species the number of diverticula is considerably higher (figs. 59, 63), from nineteen to more than forty. The diverticula are curved at the end and densely crowded together in one species.

Remarks. Pilsbry (1934) published pictures of the male copulatory organ of *D. anatinum* drawn by H. B. Baker. In these figures there is only one flagellum shown. F. C. Baker (1945) is also of the opinion that *Drepanotrema* has one flagellum only, but that the flagellum is bifid at the end in some of the species. The statement that there is only one flagellum is certainly not true and due to unsatisfactory working methods. Sometimes only sections can show the presence of the two flagella.

Fossulorbis Pilsbry, 1934.

Material. *F. cultratum* (d'Orbigny) (the type species) from Rio Ospino at Ospino and Quebrada La Virgen, 7 km. West of Guanare, both in State Portuguesa, Venezuela. (Coll. by the author 28 March 1953.)

Morphology. Discoidal shell similar to that of *Anisus*. The whorl is always covering the preceding one to some extent. The periphery is carinate.

The mantle lobe (fig. 64) is of moderate size and is bifurcated. The pseudo-branch, on which the anal pore is situated, is small. There are no renal, dorsal or rectal ridges. The whole jaw, dorsal and lateral parts, consists of small free pieces. The salivary glands are sausage-shaped and connected posteriorly.

The radula (fig. 177 r) agrees with that in *Drepanotrema*. The centrals have a couple of small lateral additional cusps. The marginals are long with lateral and posterior cusps.

The male copulatory organ (figs. 65, 66) is simple. The penis sheath is comparatively short. The penis has a terminal pore and in its distal portion there are sinuses in the tissues. The muscular pillars in the praeputium are small. Flagella are present but are extremely small and completely embedded in a strong muscle which is inserted in the upper end of the penis sheath. The vela can be regarded as two minute diverticula at the base of the penis.

The prostate consists of several unbranched diverticula from the vas deferens.

Drepanotrema.

Figs. 51-58.—*D. anatinum* (d'Orbigny).

Figs. 51-52.—Mantle opening region seen from the left. Part of the mantle cut away.

Fig. 53.—Male copulatory organ.

Fig. 54.—Cross section through the flagella.

Fig. 55-56. Longitudinally sectioned portions of the male copulatory organ.

Fig. 57.—Prostate.

Fig. 58.—Prostate and female copulatory system.

Fig. 59.—*D. lucidus* (Pfeiffer). Prostate and female copulatory system.

Figs. 60-63.—*D. aeruginosus* (Morelet).

Fig. 60.—The animal seen from the left. Upper part of the visceral sac and a piece of the mantle are removed.

Fig. 61.—Male copulatory organ.

Fig. 62.—Longitudinally sectioned portion of the male copulatory organ.

(Key to lettering, p. 542)

Figs. 64-66.

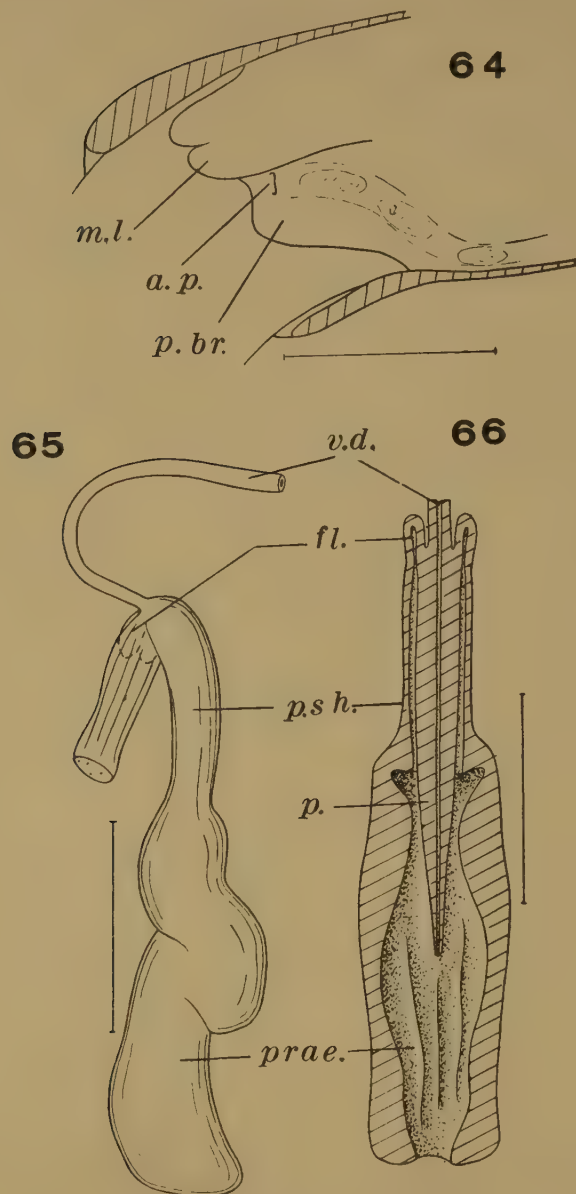
*Fossulorbis cultratum* (d'Orbigny).

Fig. 64.—Mantle opening region. A portion of the mantle is removed.

Fig. 65.—Male copulatory organ.

Fig. 66.—Longitudinally sectioned male copulatory organ.

(Key to lettering, p. 542)

Remarks. Pilsbry (1934) studied this species and published a figure by H. B. Baker of its male copulatory organ. According to this the species should have one well-developed flagellum. Apparently the muscle from the proximal end of the penis has been confused with it. The size of the "flagellum" in the figure is a point in favour of this supposition.

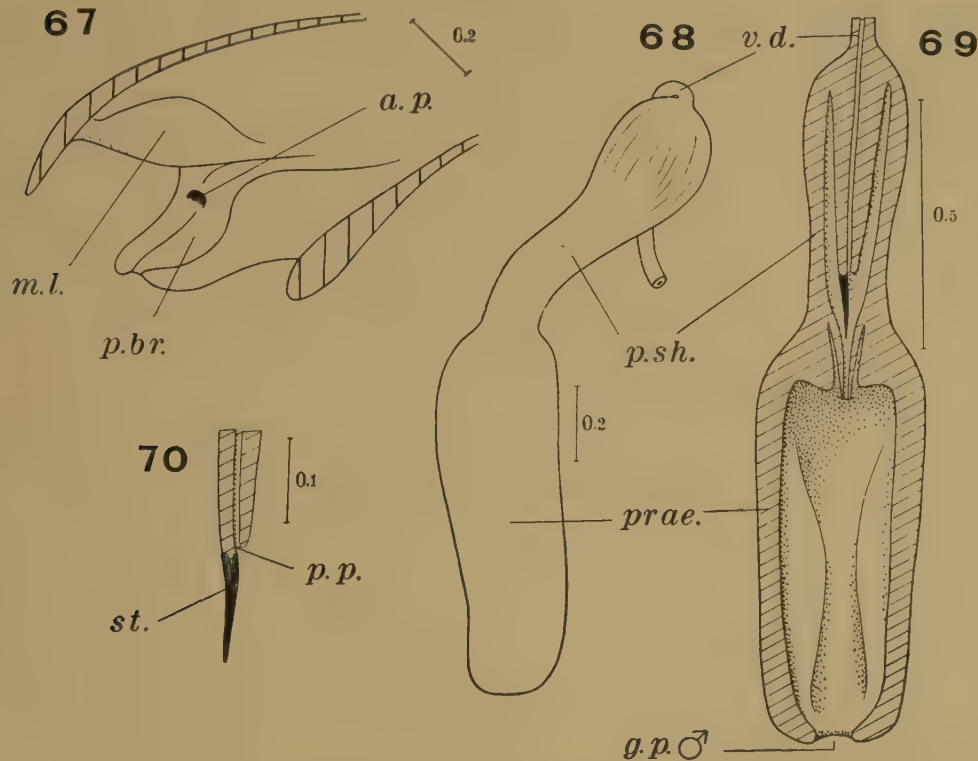
Pilsbry separated the species from *Drepanotrema* proper in the section *Fossulorbis* on conchological grounds. Baker (1945) having no spirit material of the species accepted Pilsbry's new group, retaining it as a subgenus in *Drepanotrema*. By accepting the strongly reduced flagellum as a character it may be justifiable tentatively to distinguish *Fossulorbis* from *Drepanotrema*.

Gyraulus Charpentier, 1837.

Material. *G. acronicus* (Férussac) from a stream near Björnlunda, Sörmland, Sweden. (Coll. by the author 4 Aug. 1944; Zool. Mus. Uppsala.)

Morphology. The shell is discoidal or slightly pseudo-dextral.

Figs. 67-70.



Gyraulus acronicus (Férussac).

Fig. 67.—Mantle opening region seen from the left.

Fig. 68.—Male copulatory organ. A portion of the mantle is removed.

Fig. 69.—Longitudinally sectioned male copulatory organ.

Fig. 70.—Longitudinally sectioned distal end of penis.

(Key to lettering, p. 542)

The mantle lobe (fig. 67) is of the ordinary type but is sometimes turned dorsally. The pseudobranch is well developed though not folded. The anal pore is situated on its frontal portion. There is no renal, dorsal or rectal ridge in the pallial cavity. The whole jaw is composed of large plates. The salivary glands are sausage-shaped and connected posteriorly.

The radula (fig. 178 l) has square-formed marginals without lateral cusps.

In the male copulatory organ (figs. 68, 69) the penis sheath wall is comparatively thick. A slender sarcobelum and a velum are present. The penis has a well-developed stiletto and the vas deferens opens immediately proximally to the stiletto (fig. 70).

The prostate is composed of about fourteen unbranched diverticula arising from a common duct which is branched off from the vas deferens.

Helicorbis Benson, 1855.

Material. *H. umbilicalis* Benson (the type species) from China. (Coll. 9 Sept. 1933; Zool. Mus. Berlin).—*H. mearnsi* (Bartsch) from Angalang Creek, Calinan, Davao Province, Mindanao, Philippines. (Coll. by the author 17 July 1952).

Morphology. Discoidal shell. The whorls partly embrace the preceding whorl.

The mantle lobe (fig. 73) is of ordinary shape and of moderate size. The pseudobranch, on which the anal pore opens terminally, is present only as a small papilla. There is no renal, dorsal or rectal ridge in the pallial cavity. The jaw has vertical bars. The salivary glands are sausage-shaped and joined posteriorly.

The marginals of the radula (fig. 178 o) are of the short type without lateral cusps.

The praeputium (figs. 74, 77) is voluminous in both species. In *umbilicalis* the penis sheath is very small but in *mearnsi* it is long. In both species there are two long flagella with a single layer of big rectangular or cube-shaped epithelial cells; it is probably that they have a glandular function. Outside this epithelium is a very thin sheath of connective tissue. The lumina of the flagella are in open connection with the lumen of the penis sheath.

The structure of the praeputium is different in the two species. In *umbilicalis* (fig. 75) there are two muscular pillars. One of them is very much enlarged filling up most of the lumen of the praeputium. It is formed like a muscular pillar in the distal portion only, the proximal portion being free from the praeputial wall and slowly tapering. It is rich in musculature and in the terminal portion there are some crystalline bodies and possibly some glandular cells. A duct passes through the whole organ. This duct is extremely narrow in the distal end of the organ and its opening has not been seen. In all probability, however, the duct opens through a minute terminal pore. In the opposite direction the duct goes out through the praeputial wall but enters it again after having formed some coils. After having run through the peripheral muscle layer of the wall it turns out again. This second free portion of the duct forms some coils, is thin-walled and comparatively wide. A certain part of it is very wide. It enters through the praeputial wall again but leaves it once more quite soon. Before finally entering the praeputium it forms a wide sac-like structure with thin walls. The duct opens in the praeputial lumen parallel to the penis sheath. This has fairly thick walls and a narrow lumen. It opens through a sarcobelum. The slender penis has an almost terminal opening but there is a small papilla below the pore.

In *H. mearnsi* (fig. 71) only the specialized muscular pillar is left. The duct passing through it has a distinct pore at the terminal end of the organ. In the opposite direction the duct leaves the praeputium and runs free to the point where it enters again parallel to the penis sheath. The penis is long and slender. In this species also the vas deferens opens almost terminally but a papilla (in this case cuticularized) is present below the opening.

Figs. 71-74.

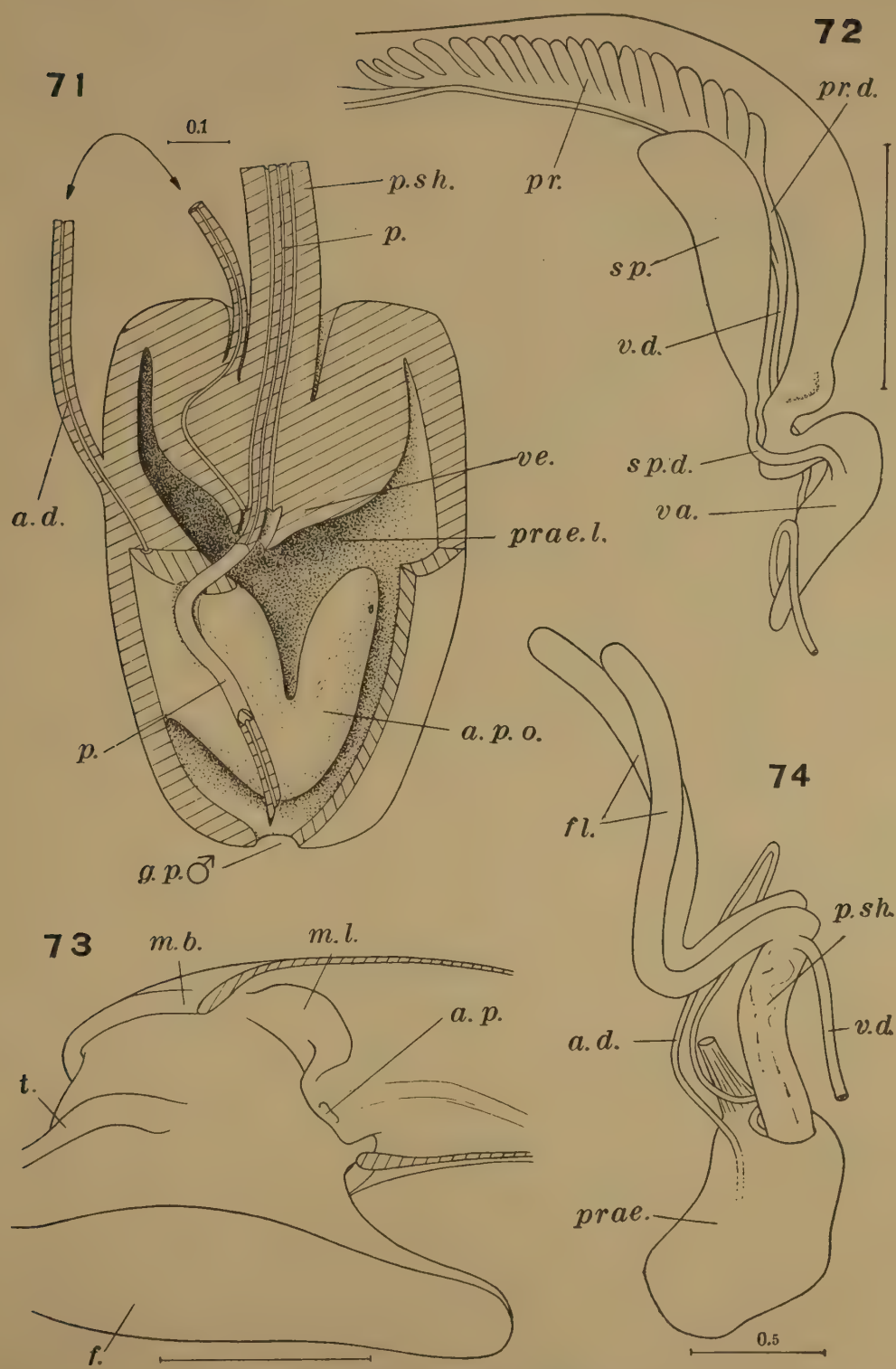
*Helicorbis mearnsi* (Bartsch).

Fig. 71.—Stereogram of male copulatory organ which is partly longitudinally sectioned. The upper part of the organ is slightly everted.

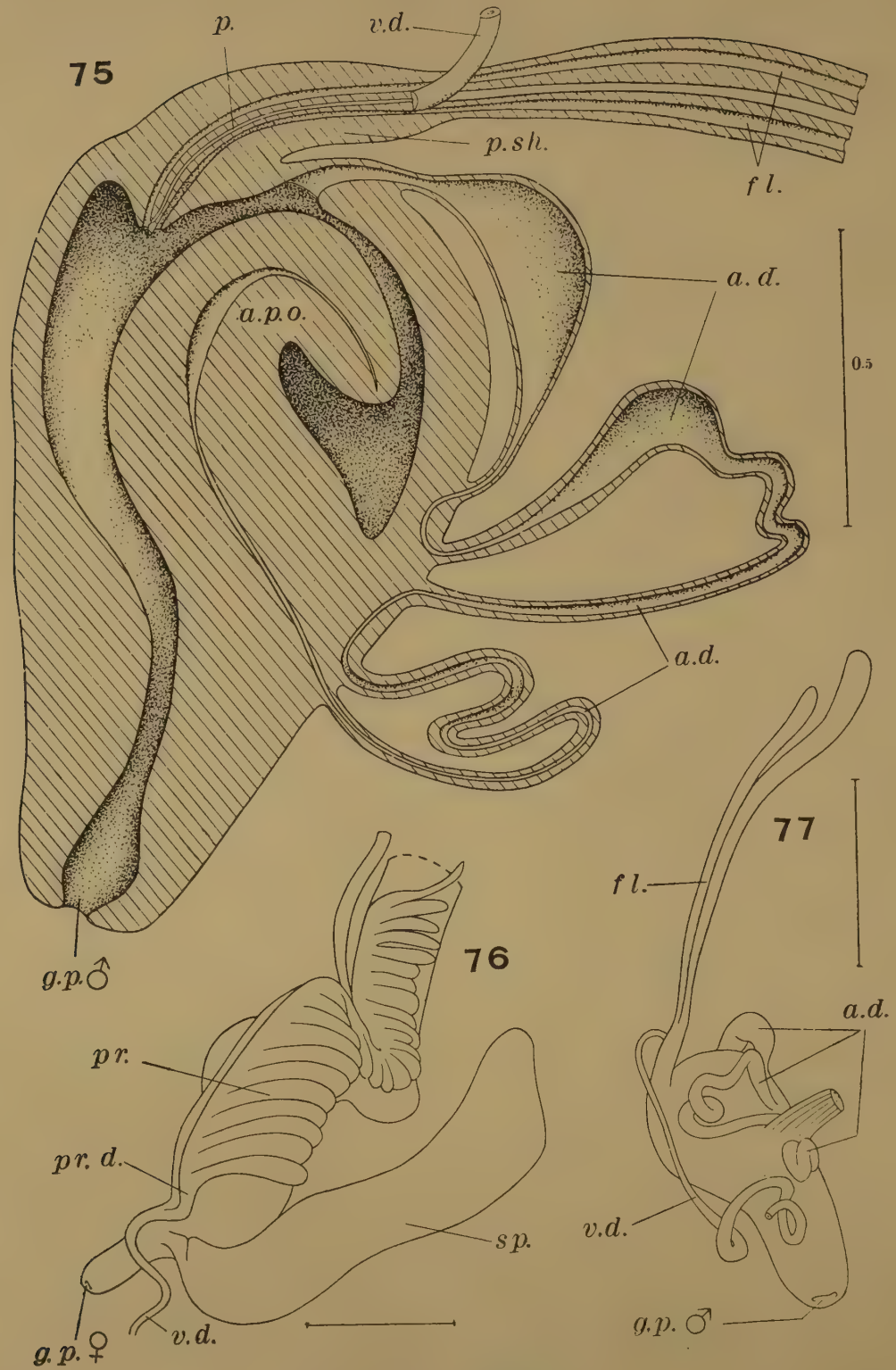
Fig. 72.—Prostate and female copulatory system.

Fig. 73.—Part of the animal seen from the left. A portion of the mantle is removed.

Fig. 74.—Male copulatory organ. The penis sheath is slightly lowered into the praecutium.

(Key to lettering, p. 542)

Figs. 75-77.



Helicorbis umbilicalis (Benson).

Fig. 75.—Longitudinally sectioned male copulatory organ.

Fig. 76.—Prostate and female copulatory system.

Fig. 77.—Male copulatory organ.

(Key to lettering, p. 542)

The prostate consists of twenty to thirty unbranched diverticular arising from a separate prostate duct (figs. 72, 76).

Remarks. Annandale *et al.* (1921) gave brief notice of the morphology of "*Hippeutis* (?) *umbilicalis*" including some remarks on the male organ. This note, which is quoted by Baker (1945), is inaccurate in several points.

Helisoma Swainson, 1840.

Material. *H. corpulentum* (Say) from Itasca Lake, Minnesota. (Coll. by Dr. E. Abdel-Malek, Ann Arbor in Oct. 1951, fixed in Bouin's fluid.)—*H. wyldi* (Tristram) from aquaria in Caracas, Venezuela (fixed in Bouin's fluid by the author 1953).

Morphology. The shell form is very variable, from sinistral with a well-developed spire, to discoidal and pseudo-dextral with at least a low, projecting spire.

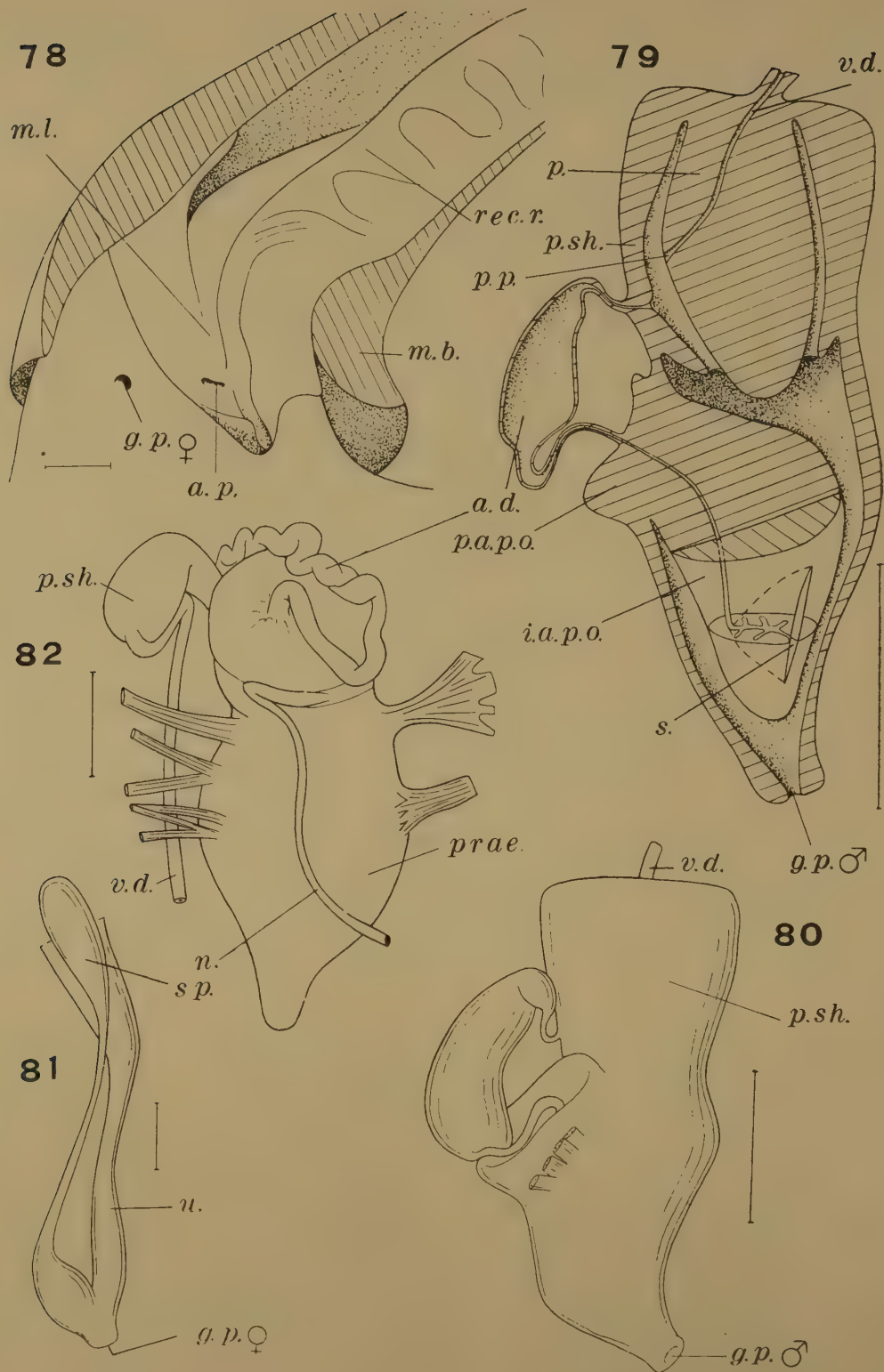
The mantle lobe and the pseudobranch (fig. 78) are fused together, the tip of the combined structure being behind the anal pore. The mantle lobe part is furrow-shaped and forms the terminal portion of the complex. According to Baker (1945), however, there is a free mantle lobe anteriorly to the lobe on which the anal pore is located in other species of *Helisoma*. In the pallial cavity there are well-developed renal, dorsal and rectal ridges. The last-mentioned one runs out on the pseudobranchial part of the lateral appendage complex, posterior to the anal pore. Within the pallial cavity the rectal ridge has well-developed, transversal, vascularized folds, probably functioning as accessory gill lamellae. The jaw has no vertical bars. The salivary glands are sausage-shaped, finely lobed and joined posteriorly.

The radula (fig. 178 *b*) has marginals of the long type with some cusps along the lateral edge.

The male copulatory organ (figs. 80, 82) of *Helisoma* consists, as Baker has pointed out, of a big praeputium and a comparatively small penis sheath (vergie sac). In addition to these there are, according to Baker, a penial gland and a gland duct leading from the lower end of the "vergie sac" to the "penial gland". A more accurate term for the organ was introduced by Abdel Malek (1952), namely praeputial organ. He also calls it hold-fast organ, referring to its function. In this paper the term praeputial organ and accessory duct will be used for the two structures.

The vas deferens enters the proximal end of the penis sheath, penetrates the penis and opens laterally on the side of the penis which is facing the proximal end of the praeputial organ (figs. 79, 83). The vas deferens does not empty terminally, the distal end of the penis being solid. The wall of the penis sheath is rather thin, mainly built up of connective tissue and some musculature. Inside it is covered by a flat or cubical epithelium, which in *H. corpulentum* produces a number of very small, cuticular spines or cusps. The connective cells are generally rounded and bladder-like, and contain often crystalline bodies. These are almost entirely dissolved because of the acid fixing fluid though remnants of them can be easily traced. The histology of the penis is similar to that of the penis sheath but its peripheral epithelium is higher with basal nuclei. It has a thin cuticle. Bundles of muscles from the penis sheath enter the penis parallel to the vas deferens. In

Figs. 78-82.



the uppermost part of the penis the musculature is dominating ; in its lower part connective tissue predominates. The central epithelium, bordering the lumen of the vas deferens, is composed of fairly high, slender, ciliated cells.

The praeputium has a very thin wall covered inside by a flattened to cubical, and, in a few places medium high, epithelium. Outside the epithelium is a layer of muscles, mostly longitudinal. Embedded in the musculature run blood vessels. The junction between the penis sheath and the praeputium has a somewhat folded wall, rich in bladder-like connective cells with crystalline bodies.

In *H. corpulentum* the projecting part of the praeputial organ is located straight proximal to the praeputium whereas the penis sheath is somewhat laterally displaced. The accessory duct leaves the penis sheath not far from the junction of the latter and the praeputium. The duct is generally flat, tightly pressed to the outside of the praeputial organ, the top of which it penetrates. The accessory duct has a fairly high epithelium with a thin cuticle and basal nuclei. It is surrounded by a moderately thick layer of circular muscles.

The internal part of the praeputial organ (the penial gland according to Baker) consists of a big pendant structure, which fills up almost the whole lumen of the projecting portion of the praeputial organ and the praeputium. The structure is of that size when not contracted. According to Baker's figures and descriptions the structure can also be contracted, occupying only a minor part of the lumen of the praeputium. The accessory duct enters the proximal end of the praeputial organ and continues as a narrow, simple duct half way down through the organ. There it joins a very complex cavity which empties through a long slit in the wall of the distal part of the organ. In *H. corpulentum* the cavity has two or three longitudinal main branches which are secondarily branched. In the three specimens studied all parts of the cavity had a very narrow lumen. The cavity extends even proximally to the level where the accessory duct enters this complex cavity. The accessory duct has an epithelium of slender cells with a thin cuticle. The epithelium of the complex cavity consists of somewhat bigger, rectangular cells with basal nuclei and a distinct cuticle. In general, the cells do not look at all like glandular cells. The portion of the complex cavity inside its distal opening has very slender epithelial cells with more or less central nuclei. They are probably glandular in function. The peripheral epithelium of the pendant part of the accessory organ is moderately high proximally and almost cube-shaped distally. This difference may be due to the different degree of extension of different portions of the organ. In the upper part of the organ the epithelium looks somewhat like a simple type of transitional epithelium. The epithelium wears a thin cuticle.

Helisoma.

Fig. 78.—*H. wyldi* (Tristram). Mantle opening region. Part of the mantle is removed.

Fig. 79.—Same species. Stereogram of male copulatory organ which is partly longitudinally sectioned.

Fig. 80.—Same species. Male copulatory organ.

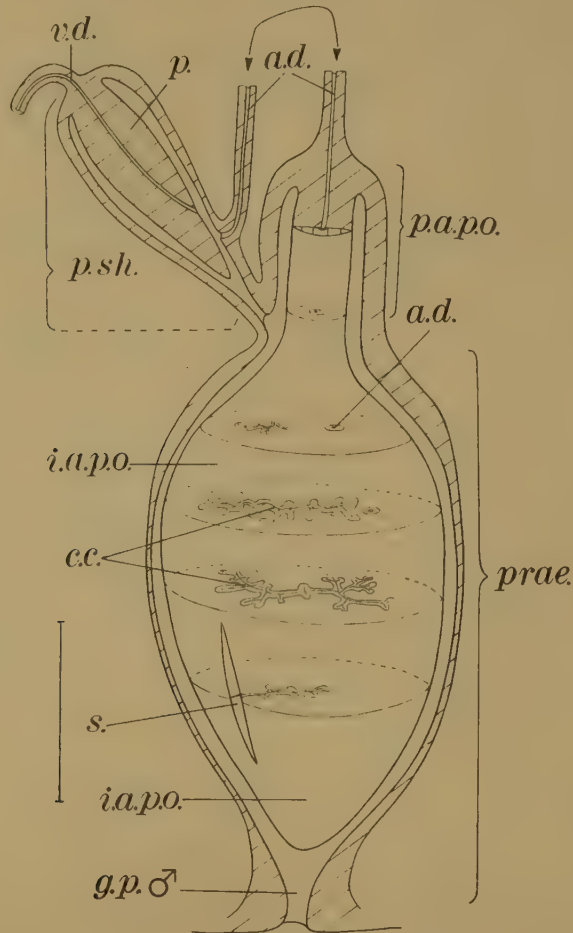
Fig. 81.—Same species. Female copulatory system.

Fig. 82.—*H. corpulentum* (Say). Male copulatory organ.

(Key to lettering, p. 542)

The accessory duct, even where running through the pendant structure of the accessory organ, is surrounded by a layer of circular muscles. This layer is particularly well developed proximally. Between this layer and the peripheral epithelium oblique, radial muscles are predominating but muscles in other directions and bladder-like connective cells with crystalline bodies also occur. All these tissues are comparatively dense in the upper part of the organ but become gradually more diffuse in a distal direction. In the most distal portion of the

Fig. 83.



Helisoma corpulentum (Say).

Stereogram of male copulatory organ.

(Key to lettering, p. 542)

organ the musculature is extremely diffuse. At least some of the muscle fibres are striated. The connective cells mentioned above do not occur in the most distal portion of the organ. There is another type of cell, however, which sometimes have an amoebocytic appearance but sometimes seem to be well delimited connective cells with a small nucleus, a very thin but distinct cell membrane and a collagenous plasma. Finally, the pendant structure also contains a net of very fine blood vessels composed of an endothelium-like tissue. In the most

distal part there are five, regularly arranged vessels but proximally there is a complex system of capillary vessels.

The prostate is composed of a large number of branched diverticula (unbranched according to Baker). There is no separate prostate duct.

Remarks. Baker (1945) has studied extensive material of *Helisoma*. There are some differences between the species, e.g. in the prostate (figs. 184–186), but all essential characters seem to be uniform for the whole group.

Baker considers that the penis pore is terminal in *Helisoma*. This is quite erroneous. It might, however, have a terminal or almost terminal position in some species. According to Baker the vas deferens in *H. trivolvis* has a central exit beyond which a small, triangular papilla extends. This may be true but in some other cases Baker has described a similar structure though serial sections show that the exit is lateral. A small, terminal, chitinous appendage has been confused with the penis pore.

Hippeutis Charpentier, 1837.

Material. *H. complanatus* (L.) (the type species) from Lake Alsen at Asker-sund, Närke, Sweden. (Coll. by the author, 9 Aug. 1944; Uppsala Univ. Museum).

Morphology. The shell is discoidal and lens-shaped.

The mantle lobe is small and the pseudobranch is extremely small or almost absent. The anal pore is located at the anterior limit of the latter. There is no renal ridge. A tiny dorsal ridge and a trace of a rectal ridge seem to occur. The jaw is composed of vertical bars. The salivary glands are comparatively short and joined posteriorly.

The marginals of the radula (fig. 178 *n*) are of the short type without lateral cusps.

In the male copulatory organ (figs. 84, 85) the praeputium is the dominating structure. There are two short flagella each built up of a single layer of epithelium. The velum is poorly developed. The penis is long and has a terminal pore. In the most distal end of the praeputium there are two slender muscular pillars. Only one of them continues up through the rest of the praeputium. In the proximal end of the praeputial lumen it forms a big, somewhat mushroom-shaped structure. It is built up mainly of musculature. According to a figure in Baker's monograph (1945) he considered this structure as homologous with a sarcobelum. It has, however, no direct connection with the region where the penis sheath merges into the praeputium. It has, on the contrary, a direct connection with a muscular pillar, and must in all probability be regarded as a special development of a muscular pillar. In his text Baker admits the structure to be attached to one of the muscular pillars. However, he calls it penial gland, which is a terminological inexactitude as it does not contain any glandular tissue.

The prostate consists of about ten, unbranched, slender diverticula from a separate prostate duct.

Figs. 84-88.

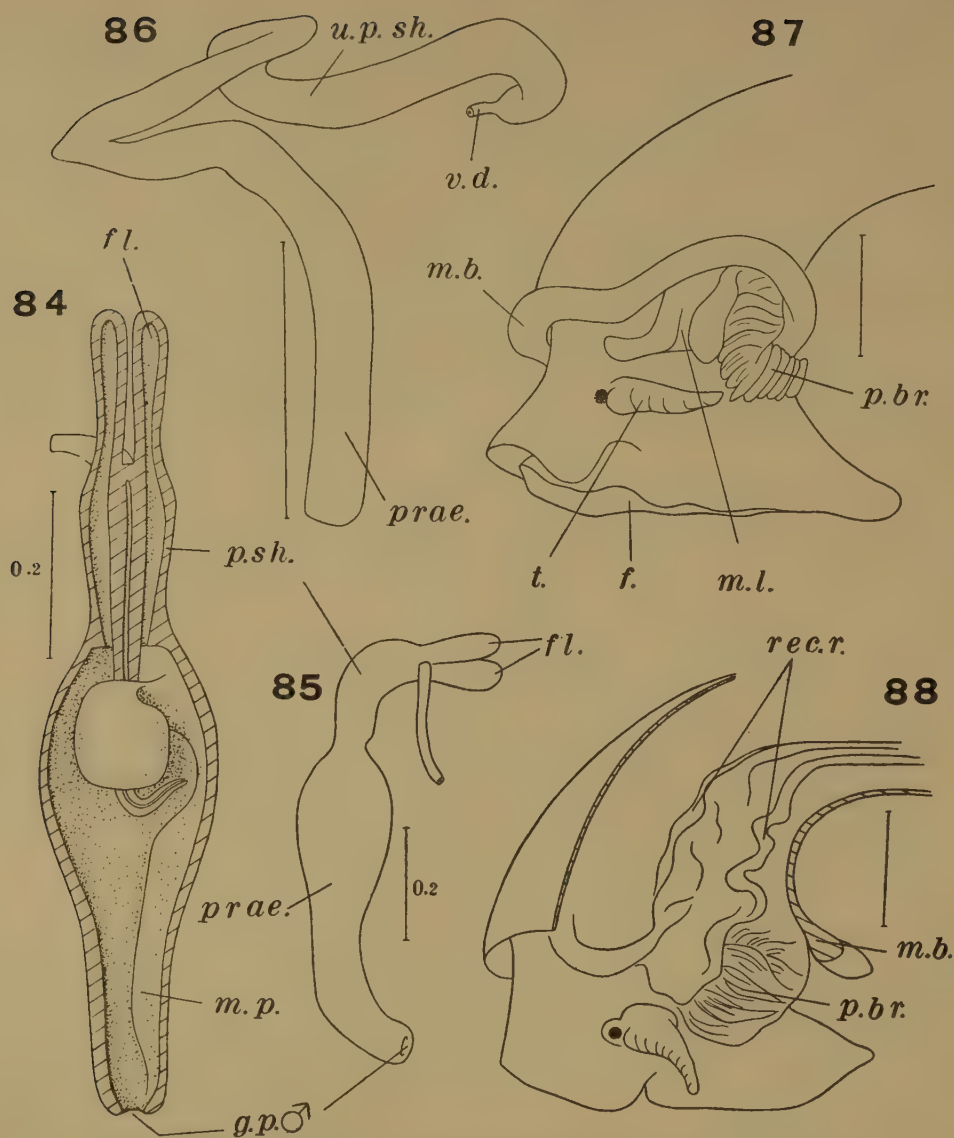
Figs. 84-85.—*Hippeutis complanatus* (Linné).

Fig. 84.—Longitudinally sectioned male copulatory organ. Only the projecting lobe in the upper part of the praeputium left intact.

Fig. 85.—Male copulatory organ.

Figs. 86-88.—*Indoplanorbis exustus* (Deshayes).

Fig. 86.—Male copulatory organ.

Fig. 87.—Lower part of animal seen from the left.

Fig. 88.—Same as in fig. 87 but part of the mantle is removed.

(Key to lettering, p. 542)

Indoplanorbis Annandale & Rao, 1920.

Material. *I. exustus* (Deshayes) (the type species) from Moradabad, India (Zool. Survey of India).

Morphology. The shell is discoidal with a slight tendency to be pseudo-dextral.

The mantle lobe (figs. 87, 88) is well-developed and furrow-shaped. The pseudobranch is big and much folded. The anal pore is located just anterior to the pseudobranch. The renal, dorsal and two parallel rectal ridges are present. One of the last mentioned reaches the pseudobranch and the other one the caudal portion of the mantle lobe. The jaw has no vertical bars. The salivary glands are sausage-shaped and joined posteriorly.

The radula (fig. 177 *b*) has marginals of the long type with both posterior and lateral cusps.

Annandale *et al.* (1921), Rao (1923) and Baker (1933), who have studied the anatomy of *Indoplanorbis*, have misunderstood the organization of the male copulatory organ. Larambergue (1939 *b*), however, has given an accurate description of it. The praeputium is comparatively short and the ultra penis sheath (*cf.* p. 471) very long (fig. 86). There is no freely pendulous penis as in *Basommatophora* in general but there is an ultra-penis which is attached to the junction between the ultra-penis sheath and the praeputium as well as to the proximal end of the ultra-penis sheath, where the vas deferens enters. The lumen of the ultra-penis sheath which surrounds the ultra-penis is only a slit in the musculature without any epithelial lining. The arrangement agrees with that in *Bulinus* and *Physopsis* (*cf.* p. 497).

The prostate consists of a great many, more or less branched, diverticula all emerging from a short, widened portion of the vas deferens.

Intha Annandale, 1922.

No spirit material of *Intha* has been available for this investigation. The following notes on its morphology are extracted from Baker's monograph.

The shell is discoidal but the body whorl completely embraces the rest of the shell.

The pseudobranch is poorly developed. There is no renal ridge. It is not mentioned whether dorsal and rectal ridges are present or not. The whole jaw is composed of vertical bars.

The radula is of the same peculiar type as in *Polypylis* and *Segmentina* (*cf.* figs. 178 *p* and *r*). The marginals are of the short type without lateral cusps.

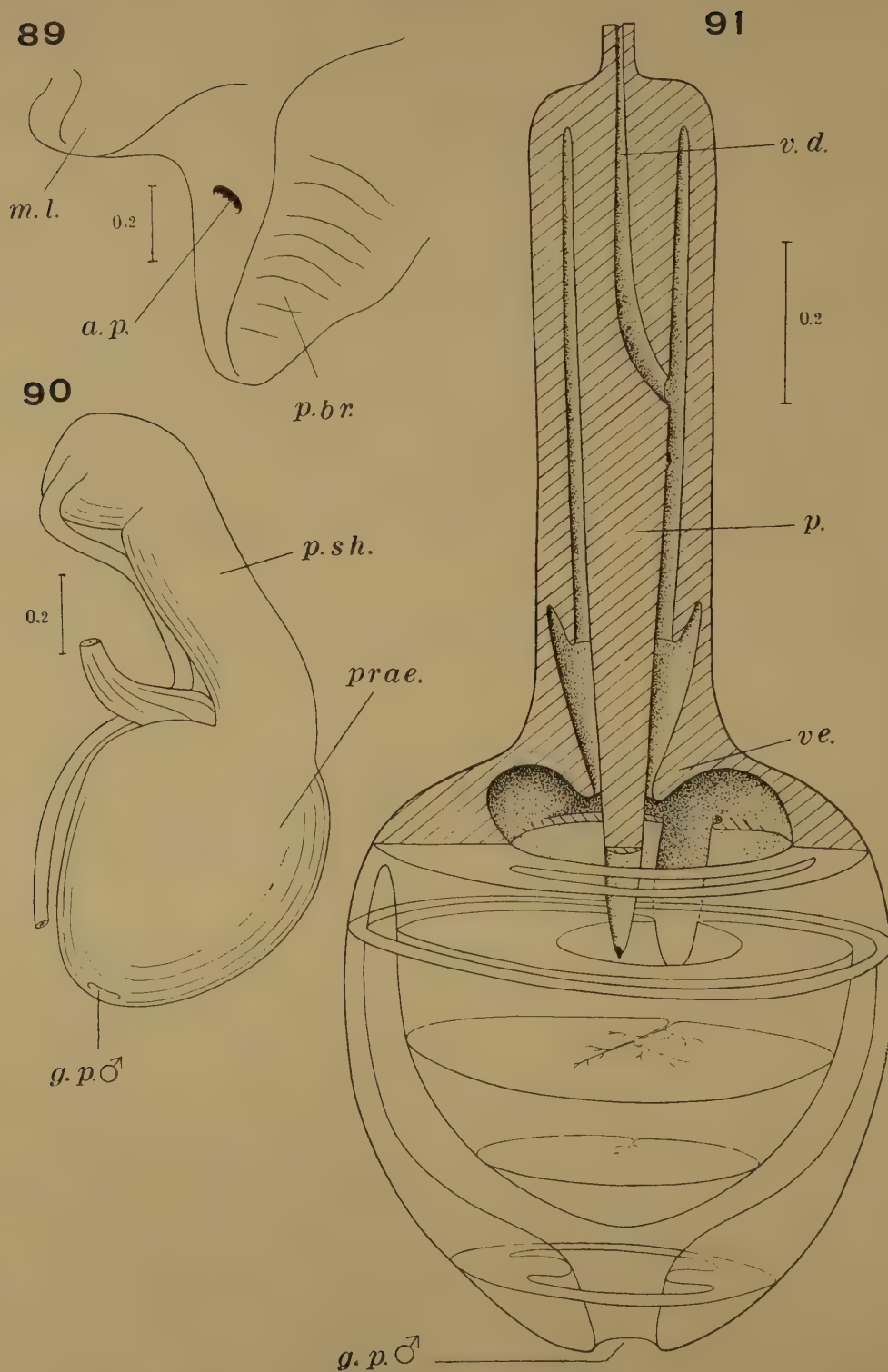
In the male copulatory organ there are two well-developed flagella with glandular tissue. There is an accessory duct connecting the lumen of the proximal end of the praeputium with an internal pendant structure in the praeputium via a loop outside the whole praeputium. The arrangement of this duct seems to be like that of the corresponding duct in *Polypylis*. According to Baker the narrow penis has a terminal exit and a very small papilla at one side of the opening. A similar arrangement is present in *Segmentina*. The prostate consists of six fairly big diverticula from a prostate duct.

Menetus H. & A. Adams, 1855.

Material. *M. opercularis* (Gould) (the type species) from a creek South of Osborn Cabin, Sugar Island, Chippewa Co., Michigan. (Coll. by H. van der Schalie, 23 July 1951).

Morphology. Shell largely discoidal but with a tendency of pseudo-dextrality.

Figs. 89-91.



Menetus opercularis (Gould).

Fig. 89.—Mantle opening appendages seen from the left.

Fig. 90.—Male copulatory organ.

Fig. 91.—Male copulatory organ. Upper portion longitudinally sectioned, lower portion stereogramatic (for explanation: compare the text).

(Key to lettering, p. 542)

A furrow-shaped mantle lobe of ordinary size is present (fig. 89). The pseudo-branch is fairly big and its posterior half bears low, rounded, transverse folds. The anal pore opens on its anterior portion. There is no renal ridge, but a small dorsal ridge and a rectal ridge are present. The jaw has no vertical bars. The fairly long salivary glands are connected posteriorly.

The marginals of the radula (fig. 178 e) are of the long type with cusps also along the lateral edge.

The male copulatory organ (figs. 90, 91) has a praeputium which is slightly shorter but twice as broad as the penis sheath. According to Baker (1945) the outline of the complex is very different. The lumen of the penis sheath is almost filled up by the penis. The vas deferens is fairly wide inside the penis; its pore is located above the middle of the penis, the distal portion of this being solid and mainly built up of transverse muscles. Baker mentions that the penial pore is terminal. Its epithelial cells are cube-shaped. There is a very small chitinous point at the tip of the penis. A sarcobelum and a velum are present. The lumen of the praeputium is to a great extent filled up by a special structure. This is what Baker called penial gland though it does not look like a gland at all; it is pendant from the proximal portion of the praeputial wall. The structure is somewhat bowl-shaped with extremely thick walls and a small concavity. There is a slit along one side of the structure. The slit is widely open proximally but almost closed distally. The exact form of the concavity or lumen of the structure is not clearly visible in the material available. However, the general pattern of the organ is in all probability correctly interpreted. Histologically the pendant structure is mainly built up of muscles orientated in different directions and of some connective tissue. Crystalline bodies occur in the latter. Whether the epithelium towards the lumen or concavity of the structure contains glandular elements cannot be stated. In the distal end of the praeputium, near the male genital pore, there are two small but distinct muscular pillars.

According to Baker the prostate consists of about a dozen main diverticula arising from the vas deferens. Each main diverticulum gives off a number of branches on one side.

Remarks. The internal morphology of the male copulatory organ in *Menetus opercularis* is misunderstood in several respects by Baker (1945). Therefore it is better to ignore the divergences in the male organ between *M. opercularis* and *M. cooperi* which Baker describes.

Miratesta Sarasin & Sarasin, 1898.

Material. *M. celebensis* P. & F. Sarasin (the type species) from Lake Posso, Central Celebes. (Coll. by P. & F. Sarasin, 18 Febr. 1895; Naturhist. Mus. Basel, 1290 a).

Morphology. The shell is sinistral with a comparatively high spire. Its structure is very different from that of all other planorbids in being thick and heavy almost as in a marine shell.

The tentacles are short. The specimen at my disposal had been partly dissected previously which accounts for my inability to make certain observations. The

Figs. 92-95.

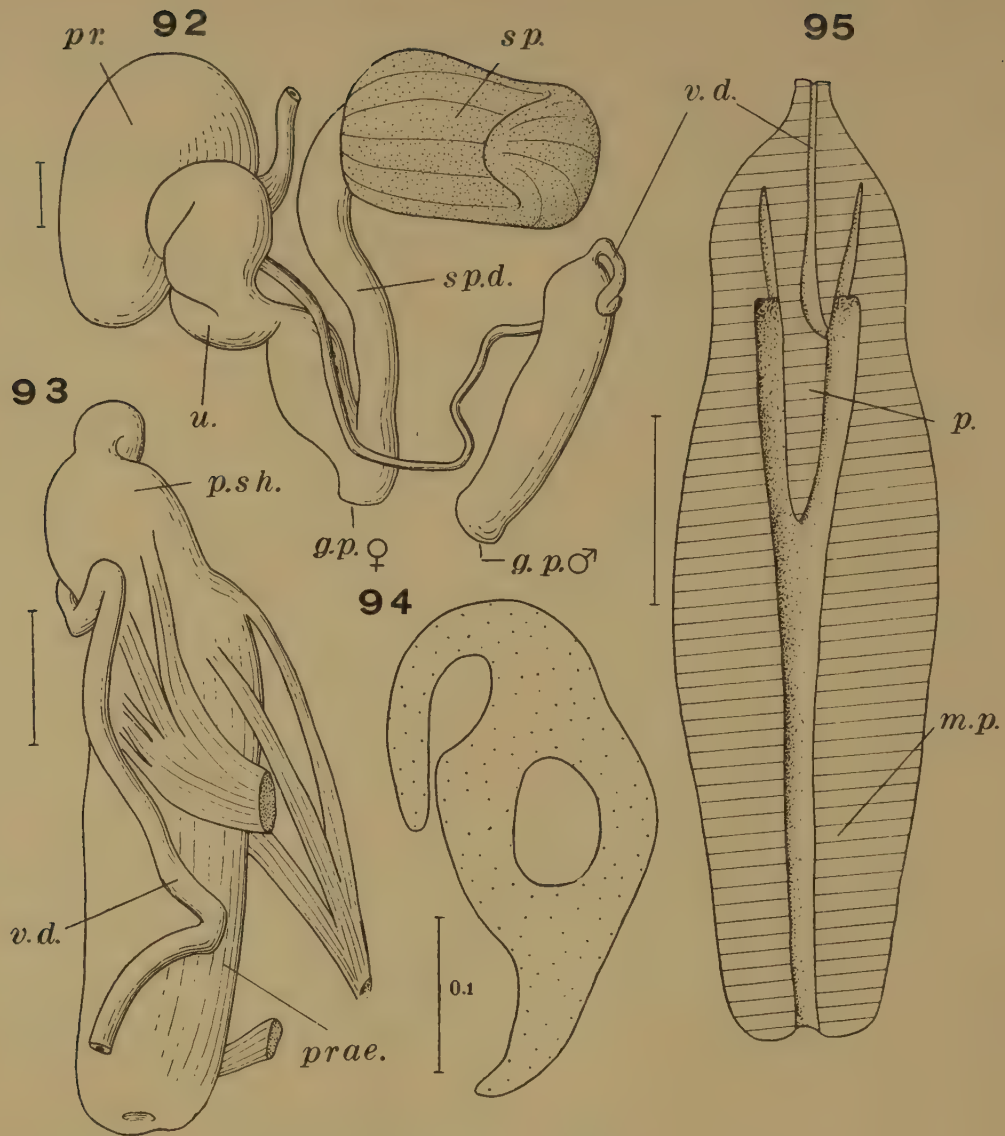
*Miratesta celebensis* Sarasin & Sarasin.

Fig. 92.—Distal parts of copulatory organs.

Fig. 93.—Male copulatory organ.

Fig. 94.—Schematic cross-section through the upper half of the penis.

Fig. 95.—Longitudinally cross-sectioned male copulatory organ.

(Key to lettering, p. 542)

form of the mantle lobe could not be checked. The pseudobranch, however, is well-developed and greatly folded. The pseudobranch as well as other parts of the anatomy have already been described by Sarasin & Sarasin (1898). They do not mention any fold formations in the pallial cavity and I have not found any. The mantle was separated from the body before I received the material which makes the observations less reliable. The jaw has no vertical bars. The lateral

parts are weakly developed. The salivary glands are rich in small lobes. It is not known if they are joined posteriorly.

The marginals of the radula (fig. 177 *f*) are of the long type, some with, others without lateral cusps.

In the male copulatory organ (figs. 93, 95) the penis sheath is very short and indistinctly marked off from the praeputium. Small muscular pillars occur. A very small velum indicates the distal limit of the penis sheath. The latter has thick walls. The vas deferens opens through a lateral pore in the penis, the distal half of the latter being solid and with a slight tendency to be triangular in section. Just above the pore there are two wing-shaped processes on the penis (fig. 94). The vas deferens is extraordinarily wide in that region. The proximal portion of the penis is circular in cross-section.

The prostate consists of a large number of diverticula from a fairly narrow band of vas deferens. The female distal genitalia are exceptionally big and the spermathecal system is peculiar (fig. 92). A coarse duct leads to the disproportionately big, zeppelin-shaped, chestnut-coloured spermatheca.

Parapholyx Hanna, 1922.

Material. Through the courtesy of Dr. Wendell O. Gregg, Los Angeles, specimens of *P. effusa* (Lea) (the type species) were collected on 10 July 1954 by Mr. R. R. Talmadge in Illamath River, Humboldt County, California, and sent to the author. The specimens were dry but could be dissected after soaking in 8 per cent tribasic sodium phosphate.

Morphology. The shell is pseudo-dextral. Mantle lobe and pseudobranch form one unit as in *Helisoma*. Rectal and dorsal ridges are present but there is no renal ridge. The jaw has no vertical bars. The salivary glands are fused posteriorly.

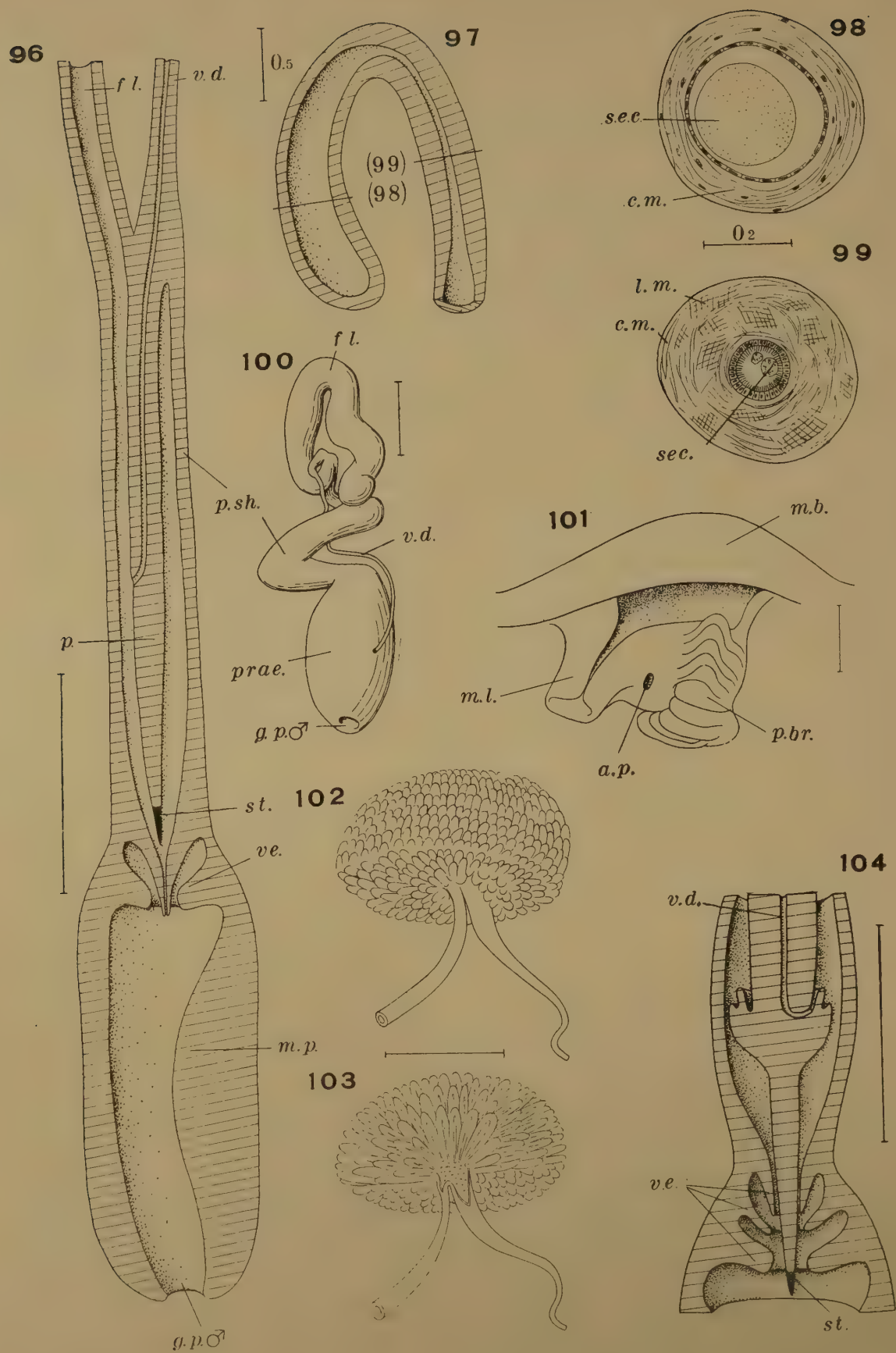
The radula (fig. 178 *g*) has long marginals with additional cusps along the lateral edge.

The male organ (figs. 174–176) has a fairly short penis sheath and penis. The vas deferens opens laterally on the penis, the lower portion of the latter being solid. From the lower portion of the penis sheath an accessory duct goes out. The free part of this duct has a thick, muscular wall. Its other end enters through the wall of the upper half of the praeputium. The duct runs in coils through a pendant structure inside the praeputium, i.e. inside an accessory praeputial organ. Just above its opening at the distal end of this structure the duct has a thick and dense sheath of musculature. The pore is surrounded by a peculiar, cuticular formation which probably works as a sucker. In addition to this accessory structure in the praeputium there are two short muscular pillars in the distal part of the praeputium and a fairly big fold formation in its proximal part not far from the velum.

The prostate is composed of a great many branched diverticula from the vas deferens.

Remarks. Baker (1945) states that the penis pore is terminal, that the upper end of the accessory duct goes out from the velum or diaphragm and that the accessory praeputial organ has a terminal gland.

Figs. 96-104.



Physastra Tapparone Canefri, 1883.

Material. Rich material of several species from the East Indies, Australia and the Pacific has been available.

Morphology. The shell is sinistral with a well-developed, sometimes high, spire.

The mantle lobe distinctly projects and is furrow-shaped (fig. 101). The pseudobranch is well-developed and greatly folded. The anal pore is located between the two structures. Renal, dorsal and rectal ridges are present. The jaw usually has strong vertical bars in its dorsal part. The lateral parts are considerably weaker. The salivary glands are lobed and connected posteriorly.

In the radula (fig. 177 *g*) the marginals are of the long type with cusps also along the lateral edge.

The male copulatory organ consists of a praeputium, a penis sheath, a penis and a flagellum (figs. 96, 100). There are one or two muscular pillars in the praeputium. Both a velum and a sarcobelum are usually present. The vas deferens opens laterally on the penis, sometimes in a circular fold (fig. 104). The distal portion of the penis is solid and bears a stiletto. The flagellum has a thick musculature (figs. 97). Its upper portion has a comparatively wide lumen with a cube-shaped or flattened, probably non-glandular epithelium (fig. 98). In the lower portion of the organ the lumen is comparatively narrow and has a ciliated epithelium (fig. 99). The size proportions and external form of the male and female copulatory organs vary to a considerable extent between the various species.

The prostate (figs. 102, 103) is built up of a large number of branched diverticula from a short U-curved section of vas deferens. The whole structure is compact and somewhat mushroom-shaped.

Remarks. For further details see Hubendick (1948 *a, b*).

Physopsis Krauss, 1848.

Material. Rich material of several species (including *P. africanus* Krauss, the type species) from Africa has been available.

Morphology. The shell is sinistral with sometimes a high but generally a low and distinct spire. It is similar to that of *Bulinus* but there is no umbilicus in *Physopsis* and the columella is twisted.

The mantle lobe (fig. 105) is well developed and furrow-shaped. The pseudo-branch consists of two main folds which are secondarily greatly folded. A very

Physastra.

Figs. 96–100.—*P. dispar* (Sowerby).

Fig. 96.—Longitudinally sectioned male copulatory organ (the main portion of the flagellum is cut off).

Fig. 97.—Longitudinally sectioned main portion of the flagellum. The numbers in brackets refer to the figures showing cross-sections through the organ.

Figs. 98–99.—Cross-sections through the upper and lower part of the flagellum respectively (*cf.* fig. 97).

Fig. 100.—Male copulatory organ.

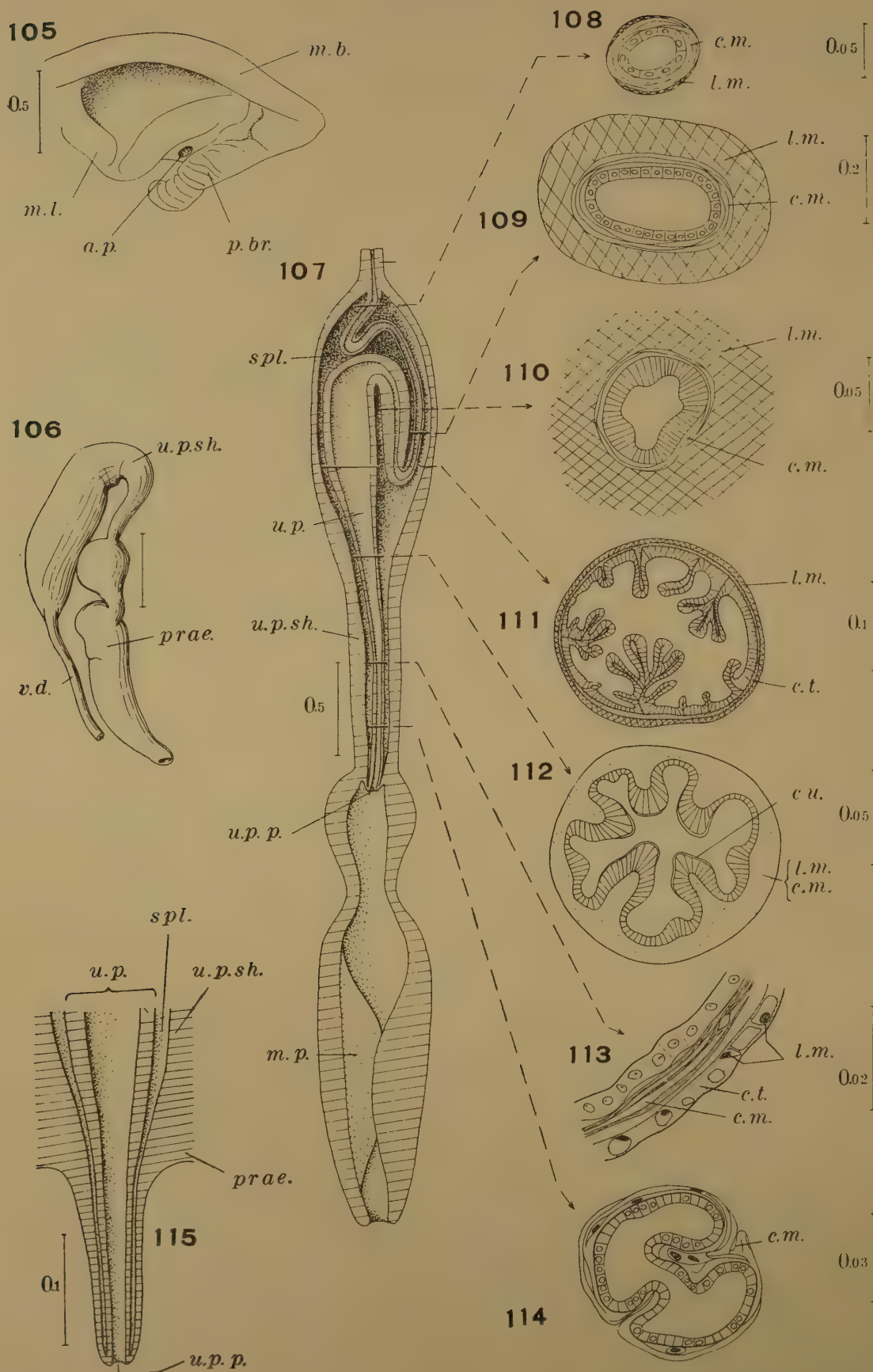
Figs. 101–103.—*Physastra* sp. from Murray River, Australia

Fig. 101.—Mantle opening region.

Figs. 102–103.—Prostata. In fig. 103 longitudinally sectioned.

Fig. 104.—*Ph. ovalinus* (Martens). Longitudinally sectioned middle portion of male copulatory organ. (Key to lettering, p. 542)

Figs. 105-115.



small renal ridge is present. There is a well-developed dorsal ridge and a rounded, fairly thick rectal ridge which reaches to the base of the pseudobranch. The anal pore is placed between the mantle lobe and the pseudobranch. The jaw is comparatively weak and has no vertical bars. The salivary glands are sausage-shaped and fused posteriorly.

The marginals of the radula (fig. 177 *d*) are of the long type with cusps also along the lateral side.

The male copulatory organ (figs. 106, 107) is similar to that in *Bulinus* and *Indoplanorbis*. Instead of a real, pendant penis there is an ultra-penis, separated from the surrounding sheath by a slit in the musculature. Consequently the ultra-penis sheath has no epithelia at all and the ultra-penis no peripheral epithelium. At its distal end the ultra-penis is connected with the junction between the ultra-penis and the praeputium (fig. 115).

Proximally the lumen of the ultra-penis sheath is wide, allowing the ultra-penis to coil inside it. Distally the lumen is narrow and the ultra-penis fills it more or less completely. The distal end of the ultra-penis has a very thin wall consisting only of a cubical epithelium and, peripherally, of a thin layer of circular muscles (fig. 114). A little more proximally the ultra-penis gets a peripheral layer of longitudinal muscles outside the circular muscle layer (fig. 113). The longitudinal muscle cells are surrounded by sheaths of connective tissue cells with thin membranes. Still more proximal the longitudinal and circular muscles are not separated but mixed (fig. 112). The epithelium has become more columnar and is furnished with a cuticle where it covers projections into the lumen. These projections are partly built up of connective tissue. Even more proximal, at about the middle of the ultra-penis, the latter and its lumen have become considerably wider and the inwardly directed projections have become taller and more slender (fig. 111). Outside the epithelium there is a layer of connective tissue and peripheral to it a layer of longitudinal muscles. The upper and coiled portion of the ultra-penis again becomes more slender and its lumen narrower. In a certain region of this part of the ultra-penis its wall has a very thick peripheral layer of longitudinal muscles (figs. 109, 110). From this region this layer tapers in both directions. The epithelium becomes cubical again and the projections into the lumen have disappeared. In the proximal end of the ultra-penis the longitudinal muscle layer is almost entirely missing (fig. 108).

The prostate is composed of a great many diverticula from a narrow band of the vas deferens.

Pingiella Baker, 1945.

No material of this genus has been available for this investigation and the relevant notes on its morphology are extracted from Baker's monograph.

Physopsis.

Figs. 105–114.—*P. africanus* (Krauss).

Fig. 105.—Mantle opening region.

Fig. 106.—Male copulatory organ.

Fig. 107.—Longitudinally sectioned male copulatory organ.

Figs. 108–114.—Schematic drawings of cross-sections through the organ in fig. 107 at the marked levels.

Fig. 115.—*P. globosus* (Morelet). The connection between ultra-penis, ultra-penis sheath and praeputium.

(Key to lettering, p. 542)

The shell is discoidal with a slight tendency to ultra-dextrality. There is no internal lamellae.

The pseudobranch is very small. There is no renal ridge. The whole jaw consists of vertical bars or plates. The salivary glands are united posteriorly.

The radula is of the same rather aberrant type found in *Polypylis* and *Segmentina*. The marginals are of the short type with no lateral cusps.

The male copulatory organ has two well-developed flagella. The penis sheath is comparatively short. The penis pore is supposed to be terminal with a small papilla just beside the opening. From the single muscular pillar a big projecting structure emerges in the praeputium (=praeputial gland according to Baker). The long and narrow accessory duct (Baker's "duct of gland") terminates on the free end of this structure. The duct runs in a long loop outside the organ and its other end opens at the upper end of the muscular pillar just below the opening of the penis sheath into the praeputium.

The prostate consists of a number of unbranched diverticula from a free prostate duct.

Remarks. The male copulatory organ of *Pingiella* is in the main almost identical with that of *Helicorbis*. There, however, the penis has a stylet and its pore has a lateral position. The free portion of the accessory duct is much shorter in *Polypylis*. This, and the aberrant form of the flagella in *Pingiella*, which Baker assigns comparative importance, are features of minor interest. The special form of the flagella in *Pingiella* as described by Baker is most probably due to a temporary functional or seasonal condition.

Planorbarius Froriep, 1806.

Material. *P. corneus* (L.) (the type species) from Altasjön, Nacka, S.E. of Stockholm. (Coll. by L. Söderberg in July 1943; Riksmuseum, Stockholm.)

Morphology. The shell is discoidal. The mantle lobe is of the ordinary well-developed furrow-shaped type (fig. 116). The pseudobranch is comparatively big but has no transverse fold formations. The anal pore is located on the base of the pseudobranch. Renal, dorsal and rectal ridges are present. The last-mentioned one has distinct transverse, vascularized folds. The jaw has no vertical bars. The salivary glands are peculiar. The parts near the buccal bulb have a large number of lobes. They continue as smooth ducts through the cerebral ring and join far behind it. There they have a small number of minute lobulae.

The marginals of the radula (fig. 178 a) are of the long type with cusps also along the lateral edge.

In the male copulatory organ (fig. 117) the penis sheath and penis are small and the praeputium is very big. The latter is about three times as long and four to five times as broad as the penis sheath. The penis has a terminal pore (fig. 118); it is built up of solid muscular tissue and its lumen has a cubical, ciliated epithelium. Where the penis sheath merges into the praeputium there is a small sarcobelum and velum. In the end of the praeputium, immediately below the velum, there are two voluminous structures connected with the praeputial wall. One of them is a solid and muscular, in outline somewhat irregular structure.

Figs. 116-119.

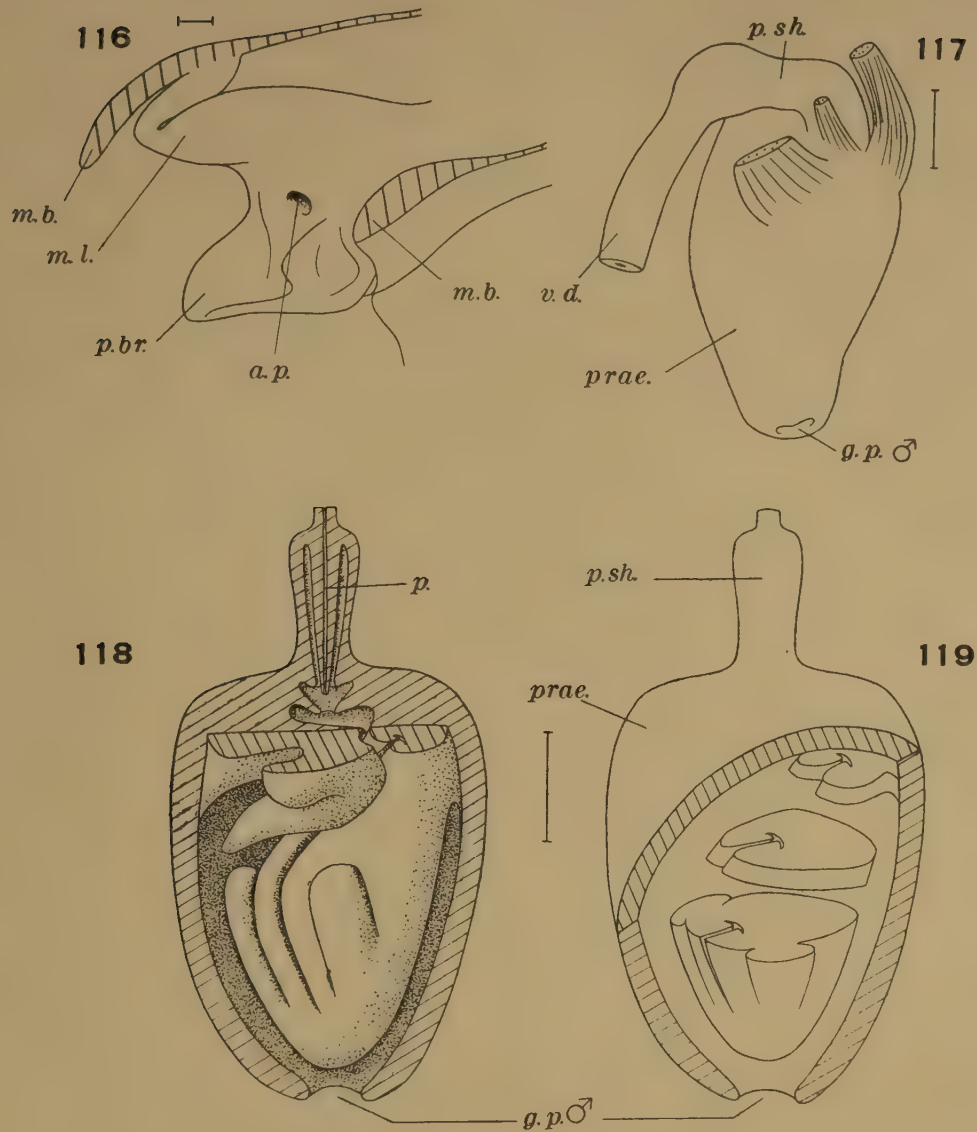
*Planorbarius corneus* (L.)

Fig. 116.—Mantle opening region. Part of the mantle cut away.

Fig. 117.—Male copulatory organ.

Fig. 118.—Male copulatory organ with penis sheath, penis and wall of praeputium longitudinally sectioned.

Fig. 119.—Diagram showing the internal structure of the dominating lobe in the praeputium.

(Key to lettering, p. 542)

It contains numerous crystalline bodies embedded in the connective tissue. One side of the organ has a thick, glandular epithelium.

The other structure (fig. 119) is bigger and fills up most of the praeputial lumen. Histologically it is similar to the first structure though the musculature is not

so dominant. There is a deep and narrow furrow along one side of the organ. At its inner end the furrow is branched forming a T in the cross-section. Along both sides of the distal half of the organ there is a blunt ridge with one free end. They are almost entirely filled up with glandular tissue.

The prostate is built up of numerous branched diverticula from a narrow band of the vas deferens or possibly from a very small appendix on the vas deferens.

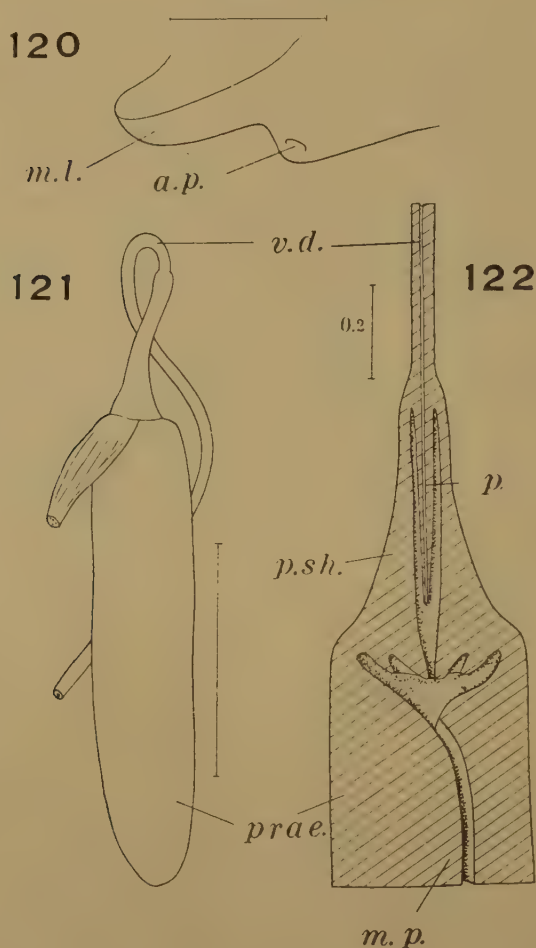
Remarks. Neither Buchner (1891) nor Baker (1945) gives a proper description of the male copulatory organ in *Planorbarius*. The terminal penial appendage shown by Baker is not always present.

Planorbis Geoffroy, 1767.

Material. *P. planorbis* (L.) (the type species) from Värtan near Stockholm. (Coll. by the author in Aug. 1951; Riksmuseum, Stockholm.)

Morphology. The shell is discoidal. The mantle lobe (fig. 120) is of the usual

Figs. 120-122.



Planorbis planorbis (Linné).

Fig. 120.—Mantle opening appendages.

Fig. 121.—Male copulatory organ.

Fig. 122.—Longitudinally sectioned proximal portion of male copulatory organ.

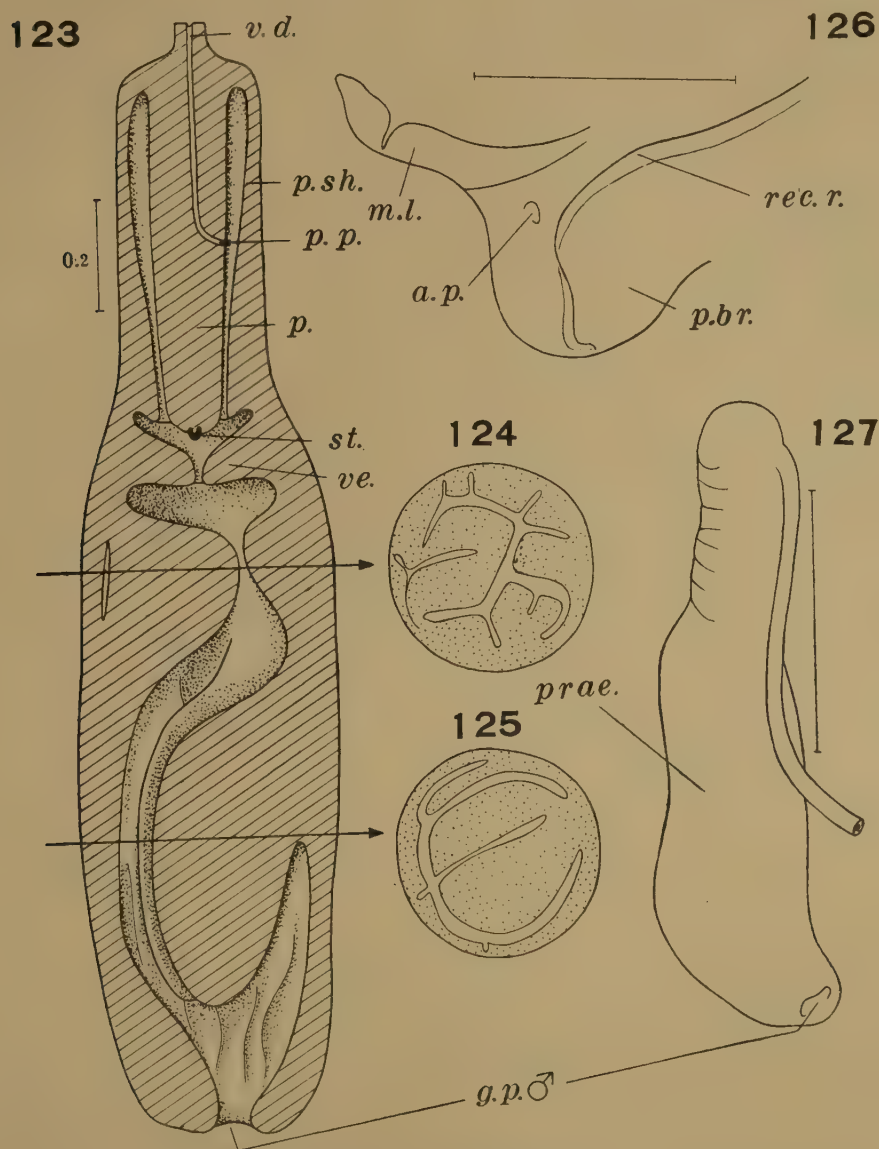
(Key to lettering, p. 542)

shape. The pseudobranch is very small and the anal pore is situated terminally on it. Renal, dorsal and rectal ridges are all absent. The jaw is composed of vertical bars. The salivary glands are sausage-shaped and joined posteriorly.

The marginals of the radula (fig. 178 i) are square-formed and lack cusps along the lateral edge.

In the male copulatory organ the penis and penis sheath are extremely small

Figs. 123-127.



Planorbula armigera (Say).

Fig. 123.—Longitudinally sectioned male copulatory organ.

Figs. 124-125.—Schematic cross-sections through the praeputium at levels marked in fig. 123.

Fig. 126.—Mantle opening appendages.

Fig. 127.—Male copulatory organ.

(Key to lettering, p. 542)

as compared with the praeputium or the male organ as a whole. The penis has a terminal pore and where the penis sheath merges into the praeputium, there is a velum and a sarcobelum. Two well developed muscular pillars are present in the praeputium. The prostate consists of a considerable number of unbranched diverticula from a separate prostate duct.

Planorbula Haldeman, 1840.

Material. *P. armigera* (Say) (the type species) from Woodspool near Ann Arbor, Michigan. (Coll. E. Abdel-Malek ; Naturhist. Riksmuseum, Stockholm.)

Morphology. The shell is discoidal with a tendency to be pseudo-dextral. The mantle lobe (fig. 126) is of the usual shape. The pseudobranch is well developed and not folded, but the rectal ridge runs out on it. The anal pore is situated anteriorly at the base of the pseudobranch. There is no renal ridge in the pallial cavity but dorsal and rectal ridges are present. The jaw has no vertical bars. The salivary glands are cylindrical and connected posteriorly.

The marginals of the radula (fig. 178 c) are of the long type with cusps also along the lateral edge.

The comparatively thick penis fills up most of the lumen of its sheath (fig. 123). The vas deferens opens laterally about half-way to the point of the penis. The distal half of the latter is solid and most of it is built up of musculature. There is a small, probably chitinous, point terminally on the penis. Both a sarcobelum and a velum are present at the point where the penis sheath merges into the praeputium. In the latter there are some folds (figs. 124, 125). The biggest occupies a considerable portion of the lumen of the organ. It consists either of two muscular pillars situated very closely together or of one muscular pillar which is cleft into two halves by a deep and narrow slit.

The prostate consists of a number of diverticula from vas deferens. The diverticula have about five branches on one side, some of the latter also dividing.

Remarks. According to Baker (1945) the penis pore is terminal and there is a gland in the praeputium.

Platytaphius Pilsbry, 1924.

Material. *P. heteropleurus* (Pilsbry & Vanatta) (the type species) from Lake Titicaca, ca. 80 m. depth. (Coll. by Percy Sladen Trust Titicaca Exp.; British Museum (Nat. Hist.), London.)

Morphology. The shell is distinctly pseudo-dextral but without a projecting spire. A mantle lobe is lacking (fig. 129). The pseudobranch is well-developed but not folded. The anal pore is located on the anterior side of the structure. There is no renal ridge in the pallial cavity, but there is a low, rounded dorsal ridge and a rectal ridge; the latter reaches out to the tip of the pseudobranch. The pallial opening is unusually narrow and hardly reaches anteriorly to the base of the pseudobranch. The jaw is weakly developed and has no vertical bars.

The marginals of the radula (fig. 177 o) are of the long type with cusps also along the lateral edge. Centrals and laterals are extraordinarily broad.

The male copulatory organ (figs. 130, 131) is simple. The penis is slender, has a terminal pore and some lacunae in its tissue. There is a weakly developed

sarcobelum and a velum joins the penis sheath and the praeputium. There are no muscular pillars in the praeputium. The prostate (fig. 128) consists of a number of small diverticula from a swollen portion of the vas deferens. More than one diverticulum can be seen at the same cross-section.

Figs. 128-131.

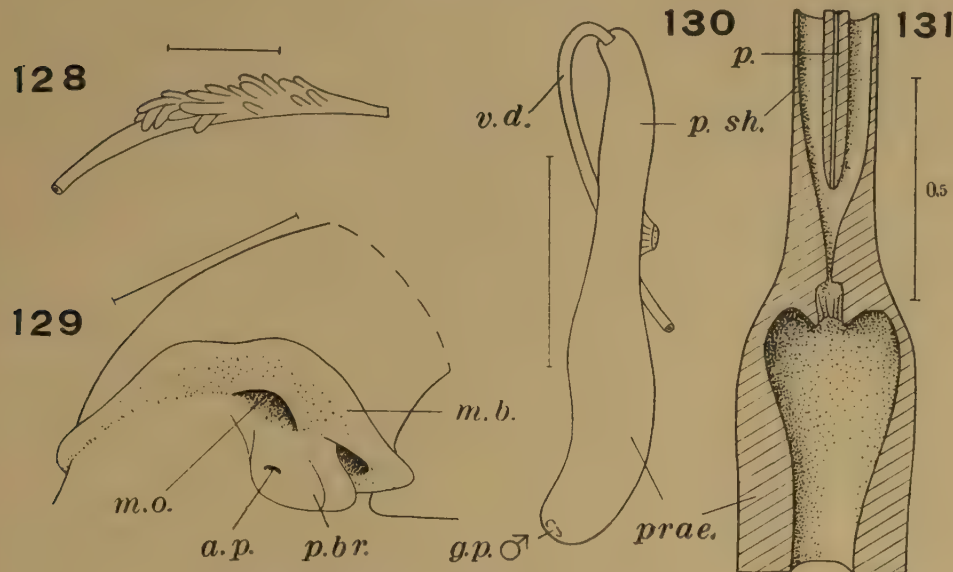
*Platytaphius heteropleurus* (Pilsbry & Vanatta).

Fig. 128.—Prostate.

Fig. 129.—Mantle opening and surrounding region.

Fig. 130.—Male copulatory organ.

Fig. 131.—Longitudinally sectioned middle portion of male copulatory organ.

(Key to lettering, p. 542)

Remarks. Baker (1945) accounts for the different opinions concerning the systematic position of *Platytaphius*. Some specialists have considered the group to be a section of *Drepanotrema*, but Baker himself rather thinks it is a distinct genus, but he adds: "What its real affinities are cannot be known until its anatomy has been investigated".

Plesiophysa Fischer, 1883.

Material. *P. ornata* Haas from Conceição, Parahyba, Brazil. (Coll. by Fr. Lenz 1935; Zoöl. Mus. Amsterdam.)

Morphology. The shell is sinistral and spiral. Most of the shell material seems to consist of periostracum.

The pallial opening is comparatively wide longitudinally (fig. 136). There is a fairly big but thin mantle lobe and dorsally to it, i.e. between the lobe and the pallial opening, there is a gill of two main folds which are secondarily folded. The anal pore is situated posteriorly to the base of the main folds. In the pallial cavity there is no renal ridge, but a low, rounded dorsal ridge is present. A rectal ridge has not been observed. The kidney and its efferent duct form an S-shaped structure. The jaw is weak and without vertical bars. Its lateral parts are not

Figs. 132-136.

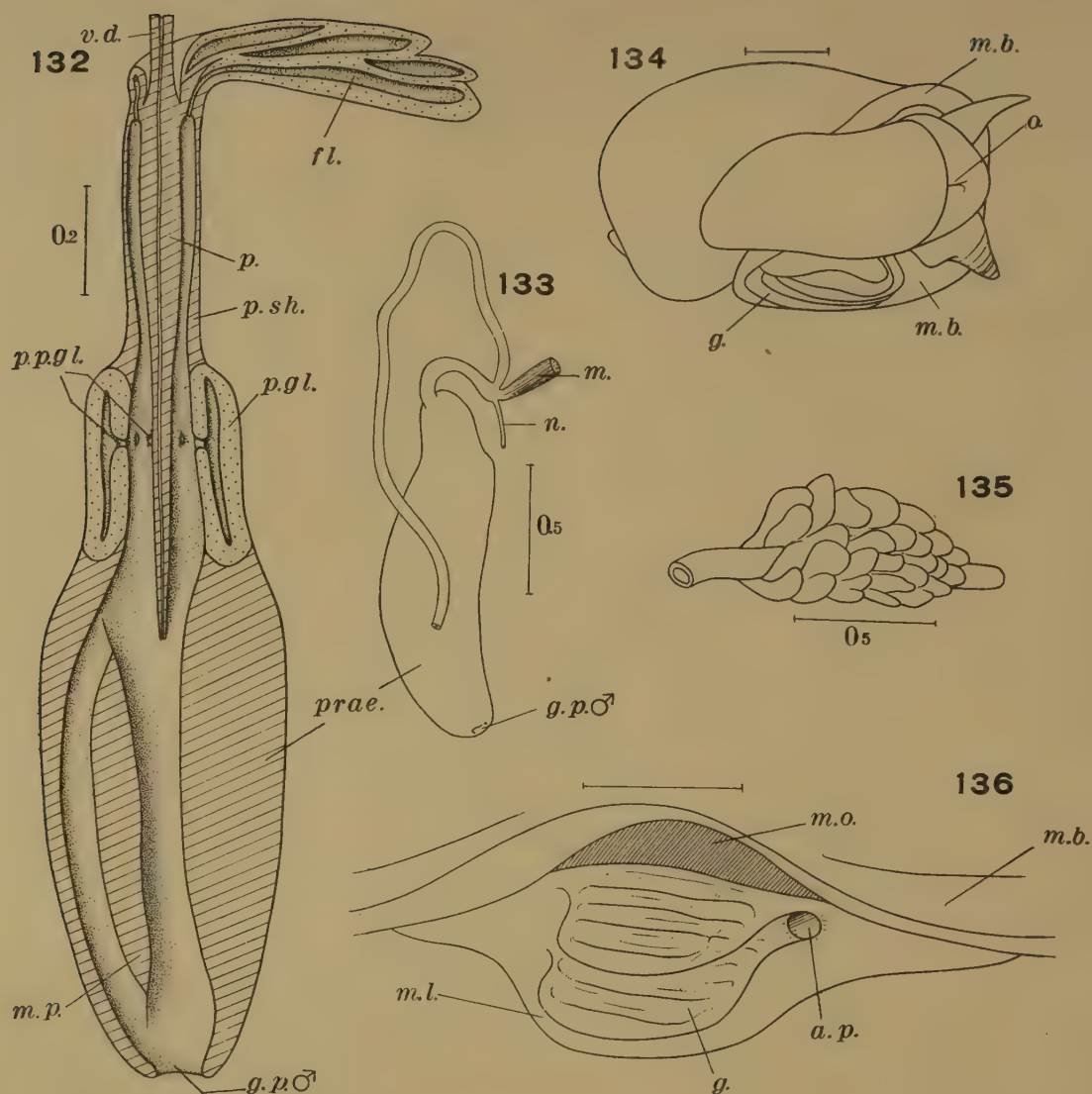
*Plesiophysa ornata* Haas.

Fig. 132.—Longitudinally sectioned male copulatory organ.

Fig. 133.—Male copulatory organ.

Fig. 134.—Ventral view of animal.

Fig. 135.—Prostate.

Fig. 136.—Mantle opening region.

(Key to lettering, p. 542)

visibly chitinized. The salivary glands are much lobed and comparatively short. They do not seem to be connected posteriorly.

The radula (fig. 177 *a*) is aberrant in having three well-developed cusps on the centrals. There are, in addition, one more minute cusp on either side. The first lateral is quadricuspid. The marginals are of the long type with cusps also along the lateral edge.

The male copulatory organ (figs. 132, 133) has a penis sheath merging into the praeputium without any sharp demarcation. Both sarcobelum and velum are lacking but in the same area there are eight radially arranged glands. The latter are fairly long and run parallel to the penis. But they communicate with the main lumen of the male organ only through a small pore in the middle portion of each gland. The glands are built up of large cells, ten to fifteen can be seen in a cross-section. The penis is long and slender and has a terminal pore. At the proximal end of the male organ there is a flagellum structure consisting of a number of glands opening into the lumen of the penis sheath around the point where vas deferens enters the penis. The glands together form a compact mass with only their ends separated from one another a little. The flagellar glands are built up of an epithelium of fairly big cells, surrounded by a thin sheath of connective tissue.

The prostate (fig. 135) is formed of a number of diverticula arising from the vas deferens. There are about four or five diverticula to be seen in one cross-section of the vas deferens.

Polypylis Pilsbry, 1906.

Material. *P. calathus* (Benson) from three different localities in Mindanao, the Philippines. (Coll. by the author 1952; Naturhist. Riksmuseum, Stockholm.)

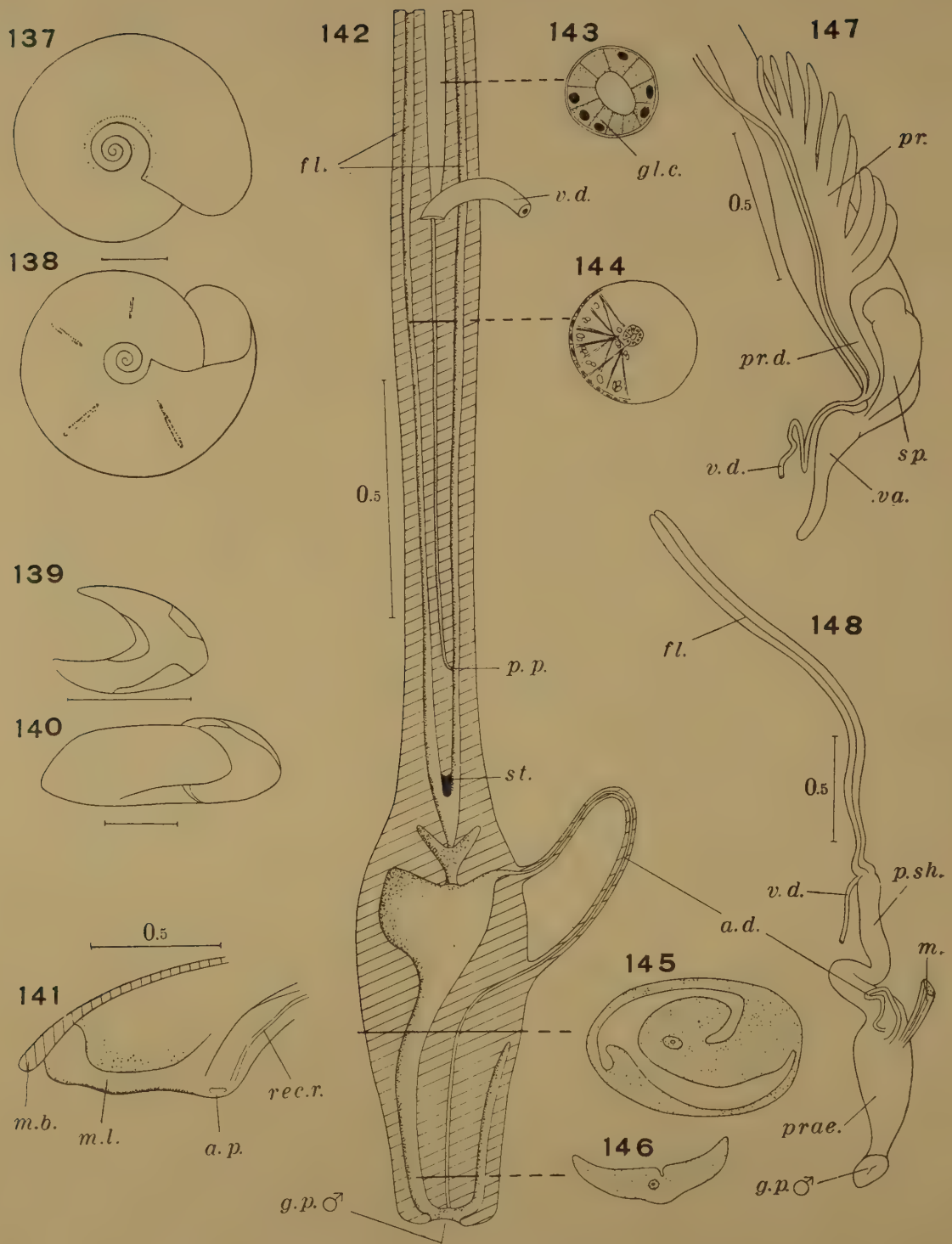
Morphology. Discoidal shell (figs. 137–140). Every whorl embraces most of the preceding whorl. There are internal lamellae in the shell (figs. 138, 139).

The mantle lobe (fig. 141) is very small and there is hardly any pseudobranch at all. There is neither a renal ridge nor a dorsal ridge but a very slender rectal ridge is present. The jaw is composed of a comparatively small number of broad, vertical bars. The salivary glands are cylindrical but comparatively short and joined posteriorly.

In the radula (fig. 178 *r*) laterals and marginals are of a special type. They both have a row of small cusps directed posteriorly. The marginals clearly belong to the short type with no lateral cusps.

In the male copulatory organ (figs. 142, 148) the penis sheath is considerably longer than the praeputium. The penis is long, filling up most of the lumen of the praeputium. The vas deferens opens laterally on the penis, leaving the distal portion of the penis solid. Its point is covered with a stylet or is at least cuticularized. The penis is comparatively rich in radial muscles (fig. 144). Two long and slender flagella are connected with the upper end of the penis sheath. They consist almost entirely of a thick, glandular epithelium (fig. 143). There is a sarcobelum and a velum at the junction between the penis sheath and the praeputium. The praeputium has two internal folds. One of them is formed like a very small muscular pillar. The other fold is pendant from one side of the upper part of the praeputial wall. A narrow canal runs through this fold. One end of the canal opens at the distal, pendant end of the fold just inside the male genital pore. After having passed longitudinally through the whole fold the canal leaves the praeputium and, after a loop outside the organ, turns back to the proximal end of the praeputium where it passes through the wall and opens just below the velum.

Figs. 137-148.



The prostate (fig. 147) consists of ten unbranched diverticula from a special prostate duct. The spermatheca is pear-shaped and opens directly into the female duct without any distinct duct of its own.

Remarks. In *P. hemisphaerula* (Benson) Baker (1945) has found one flagellum with a thicker, slightly bulbous upper end. The thicker upper end is certainly due to the functional stage of the organ. Most probably there are two flagella closely adpressed together. In *P. calathus* Baker has noticed two flagella. In *P. hemisphaerula* Baker has found a fleshy, terminal papilla below the lateral penis pore. In this species there seems to be neither accessory duct nor praeputial organ.

Promenetus Baker, 1935.

Material. *P. exacuus* (Say) (the type species) from near Ypsilanti, Michigan. (Coll. E. Abdel-Malek ; Naturhist. Riksmuseum, Stockholm.)

Morphology. The shell is slightly pseudodextral. A distinct separate mantle lobe seems to be lacking (fig. 149). The pseudobranch is well developed and the anal pore is situated anteriorly on it and close to its base. The rectal ridge runs more than half-way out on it. There is no renal ridge in the pallial cavity but there is a dorsal one. The jaw has no vertical bars. The salivary glands are sausage-shaped and connected posteriorly.

The marginals of the radula (fig. 178 *d*) are of the longtype with cusps also along the lateral edge.

In the male copulatory organ (figs. 151, 153) the penis sheath is long and thick. Its walls are thin but the penis fills up almost all its lumen. The vas deferens opens laterally on the proximal half of the penis, the distal part of the latter being solid. The penis is filled with a fairly diffuse musculature. Its epithelium is flattened and bears a thin cuticle. There is a very small chitinous structure at the tip of the penis. A number of very fine but distinct notches runs longitudinally along the surface of the penis. A sarcobelum is present where the penis sheath enters the praeputium. There is no velum of the ordinary shape but there are some folds in the corresponding region of the praeputium (fig. 154). Almost the whole lumen of the praeputium is filled up with a structure which Baker calls penial gland. It consists of two folds, similar to muscular pillars, which are joined at their distal ends, not far from the male genital pore. The folds are attached to the wall of the praeputium with only very tiny connections. More

Polypylis calathus (Benson).

Fig. 137.—Right side of shell.

Fig. 138.—Left side of shell.

Fig. 139.—Cross-section of whorl showing the lamellae.

Fig. 140.—Ventral view of shell.

Fig. 141.—Mantle opening region. Part of the mantle cut away.

Fig. 142.—Longitudinally sectioned male copulatory organ.

Figs. 143–146.—Cross-sections through various parts of the male organ at levels indicated in fig. 142.

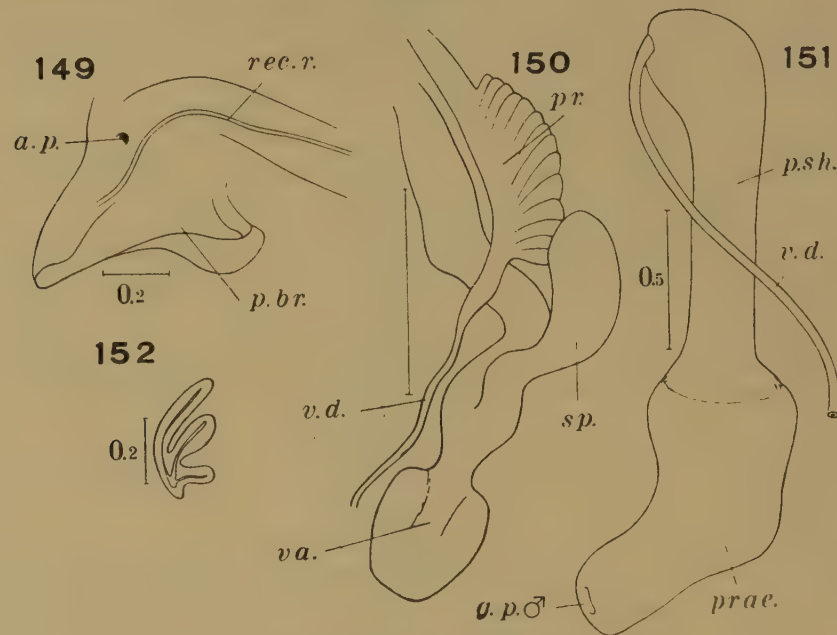
Fig. 147.—Prostate and female copulatory system.

Fig. 148.—Male copulatory organ.

(Key to lettering, p. 542)

distally the slit separating the folds does not reach to the base of the folds, thus giving them a common base. Still more distally the structure loses its connection with the praeputial wall and hangs completely free. From the slit separating the proximal portions of the folds there are branches into the two folds. Distally the innermost part of the slit is separated from the rest of it and continues as a short, blind duct.

Figs. 149–152.



Promenetes exacuus (Say).

Fig. 149.—Mantle opening appendages.

Fig. 150.—Prostate and female copulatory system.

Fig. 151.—Male copulatory organ.

Fig. 152.—Cross-section through prostate.

(Key to lettering, p. 542)

The prostate (figs. 150, 152) has a number of diverticula from the vas deferens which give off some branches on one side.

The distal end of the vagina (fig. 150) is broad, having two strongly thickened patches in its wall. This character may, perhaps, be of mere specific range.

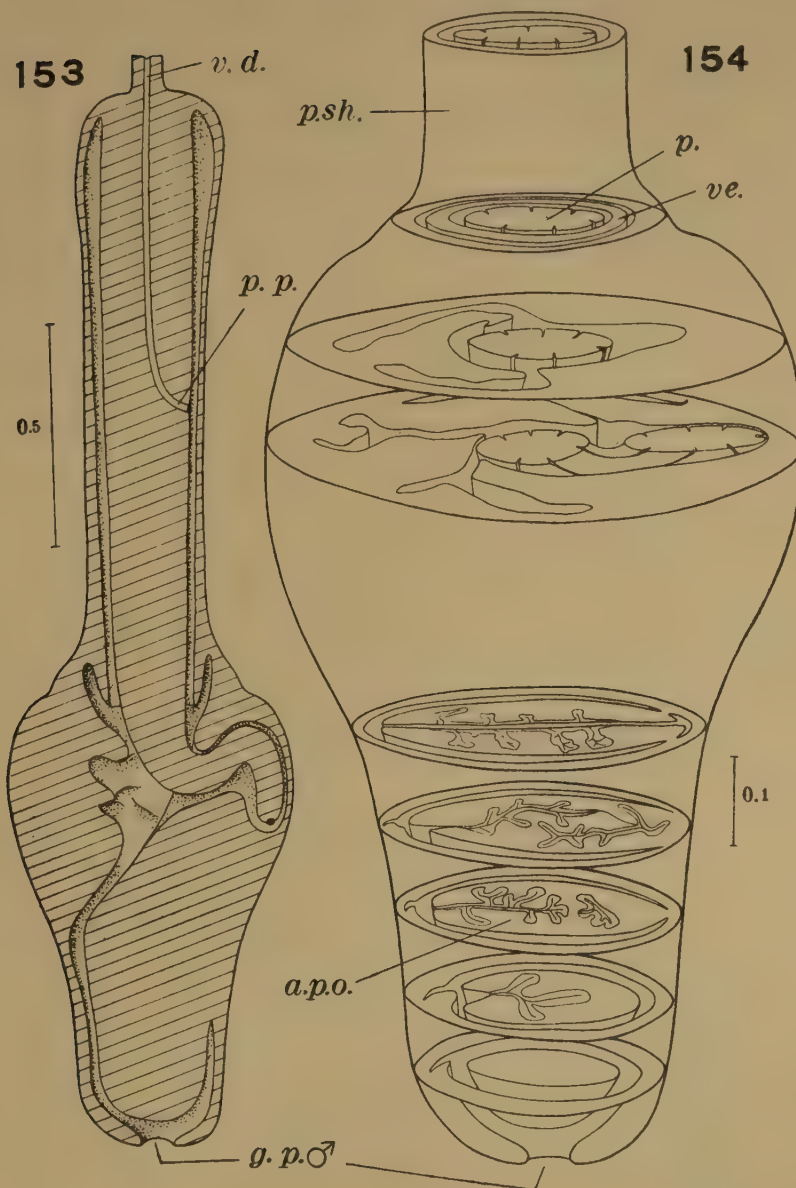
Remarks. Baker (1942) has confused the chitinous tip of the penis with a papilla and the penis pore. The interior of the praeputium is misinterpreted as there is no gland.

Segmentina Fleming, 1817.

Material. *S. nitida* (Müller) (the type species) from Stehag, Scania, Sweden. (Coll. by W. Lilljeborg in 1878 ; Zool. Mus. Uppsala.)

Morphology. The shell is discoidal and similar to that of *Polypylis*. Transverse callus formations occur at different places in the last whorl. At each place there are usually three lamellae opposite one another.

Figs. 153-154.



Promenetes exacuus (Say).

Fig. 153.—Longitudinally sectioned male copulatory organ.

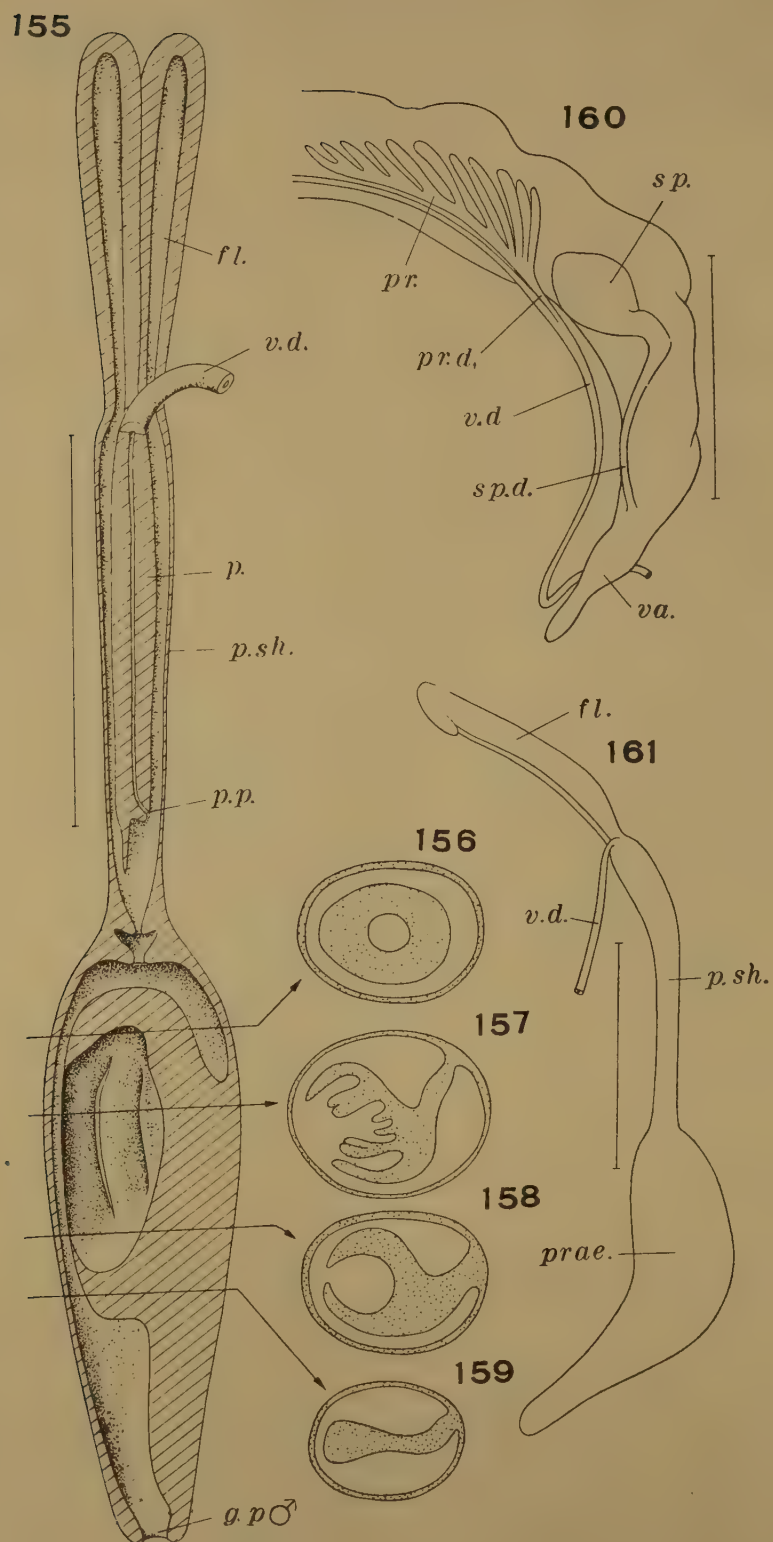
Fig. 154.—Stereogram of the distal half of male copulatory organ.

(Key to lettering, p. 542)

There is a well-developed, furrow-shaped pallial lobe. The pseudobranch is very small. The anal pore is situated on it. Renal, dorsal and rectal ridges do not occur. The jaw consists of a number of vertical bars. The salivary glands are short but connected posteriorly.

The radula (fig. 178 *p*) is of the same special type as in *Polypylis*. The marginals belong to the short type with no lateral cusps.

Figs. 155-161.



The male genital organ (figs. 155, 161) has two flagella consisting of an epithelium of big cells inside a very thin sheath of connective tissue. Their sinuses are connected with that of the penis sheath. The penis sheath has thin walls. The very thin epithelium of the penis is covered by a cuticle. The vas deferens opens terminally but somewhat excentrically. The penis continues distally beyond the pore with a thin papilla which is not chitinous. Both a distinct sarcobelum and velum occur. The praeputium is thin-walled but has one big muscular pillar of a peculiar shape (figs. 156-159). It is connected with the praeputial wall through a slender neck. Opposite the junction the structure is strongly enlarged and the surface is deeply concave. In the bottom of the concavity there are four projecting folds, probably covered with a glandular epithelium. The available material was not well-preserved enough to allow a positive assertion.

The prostate (fig. 160) consists of a number of unbranched diverticula arising from a separate prostatic duct.

Syrioplanorbis Baker, 1945.

Baker (1945) quotes the original description of *Planorbis libanicus* Westerlund which Westerlund designated as the type species of his genus *Heterodiscus*. As the name *Heterodiscus* was praeoccupied Baker replaced it with *Syrioplanorbis*. Without a figure of the type species of this monotypic genus Baker could not place it taxonomically. Though Baker admits that only the study of the animal can lead to a positive conclusion, he supposes that *Syrioplanorbis* is closely related, if not congeneric, with *Afroplanorbis*. The author of this paper has had the opportunity to examine the shell of "*Planorbis libanicus*" from the Westerlund collection in Gothenburg. The shell shows quite clearly that it has to be classified with little doubt as a *Biomphalaria*, which has proved to be congeneric with *Afroplanorbis*.

Taphius H. & A. Adams, 1855.

Material. *T. andecolus* (d'Orbigny) (the type species) from Uruñi Bay, Lake Titicaca, 9 July 1937; *T. montanus* (d'Orbigny) from Capachica, Lake Titicaca, 15 Sept. 1937; a transitional form between the two above mentioned "species", from Taquiri Island. Lake Titicaca, 30 July 1937. All the material collected by the Percy Sladen Trust Expedition to Lake Titicaca and determined by Dr. F. Haas, Chicago. (British Museum (Nat. Hist.), London.)

Morphology. The shell is discoidal. The mantle lobe (fig. 163) is very small. The pseudobranch is well developed. The anal pore is located on its dorsal surface anterior to the end of the rectal ridge. Beside the rectal ridge there is a dorsal ridge in the pallial cavity but no renal one. The jaw is weakly developed and has

Segmentina nitida (Müller).

Fig. 155.—Longitudinally sectioned male copulatory organ.

Figs. 156-159.—Cross-sections through the praeputium at levels marked in fig. 155.

Fig. 160.—Prostate and female copulatory system.

Fig. 161.—Male copulatory organ.

(Key to lettering, p. 542)

Figs. 162-165.

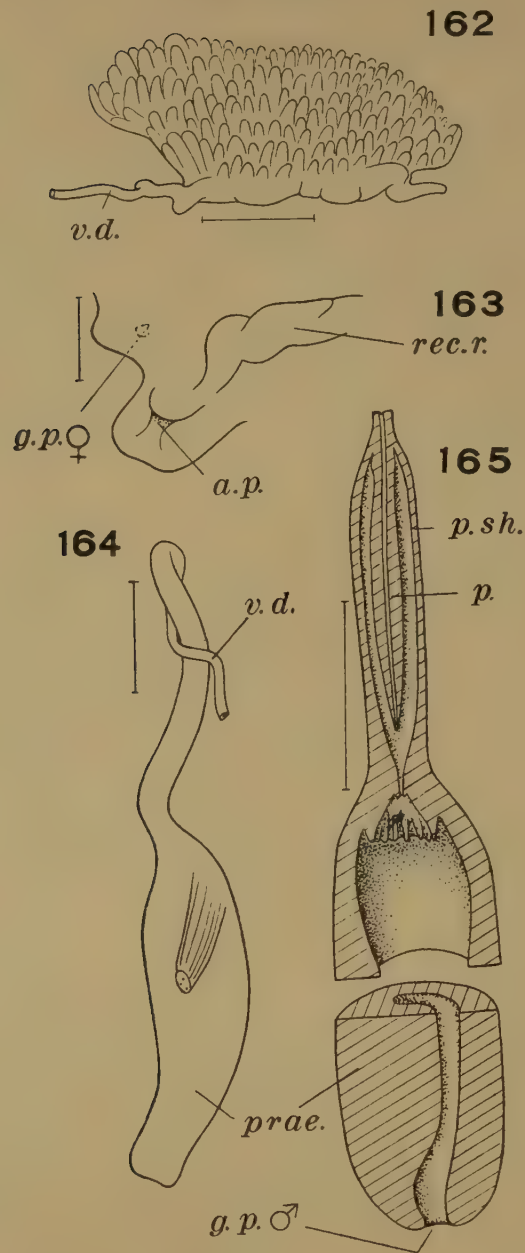
*Taphius montanus*—*T. andecolus* (d'Orb).

Fig. 162.—Prostate.

Fig. 163.—Mantle opening region.

Fig. 164.—Male copulatory organ.

Fig. 165.—Longitudinally sectioned male copulatory organ.

(Key to lettering, p. 542)

no vertical bars. The salivary glands are slightly lobated and connected posteriorly.

The marginals of the radula (fig. 177 *n*) are of the long type with cusps also along the lateral edge.

The male copulatory organ (figs. 164, 165) is simple. The penis is slender and has lacunae in its tissue. The proximal end of the lumen of the penis sheath

forms a number of small, blind ending tubes similar to the proximal chambers in *Lymnaea*. Their epithelium is probably glandular. This is the only planorbid in which proximal chambers have been observed. At the junction between the penis sheath and the praeputium there is a very small sarcobelum and a folded velum. There is one muscular pillar in the praeputium.

Figs. 166-171.

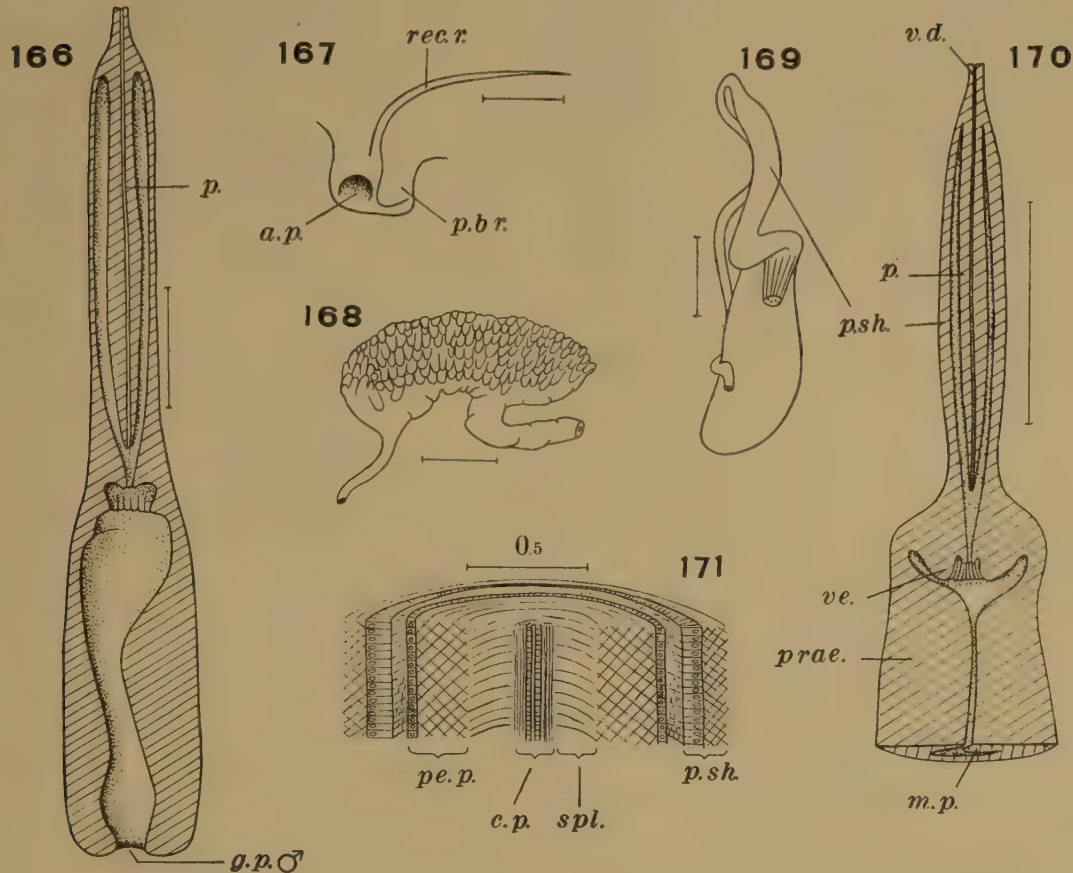
*Tropicorbis*.Figs. 166-169.—*T. canonicus* (Cousin).

Fig. 166.—Longitudinally sectioned male copulatory organ.

Fig. 167.—Mantle opening appendage.

Fig. 168.—Prostate.

Fig. 169.—Male copulatory organ.

Figs. 170-171.—*T. pallidus* (Adams).

Fig. 170.—Longitudinally sectioned male copulatory organ.

Fig. 171.—Semischematic stereographic diagram of a section of penis and penis sheath.

(Key to lettering, p. 542)

The prostate (fig. 162) is composed of a number of branched diverticula from a swollen portion of vas deferens. More than one diverticulum can be seen in a cross-section through the organ.

Figs. 172–176.

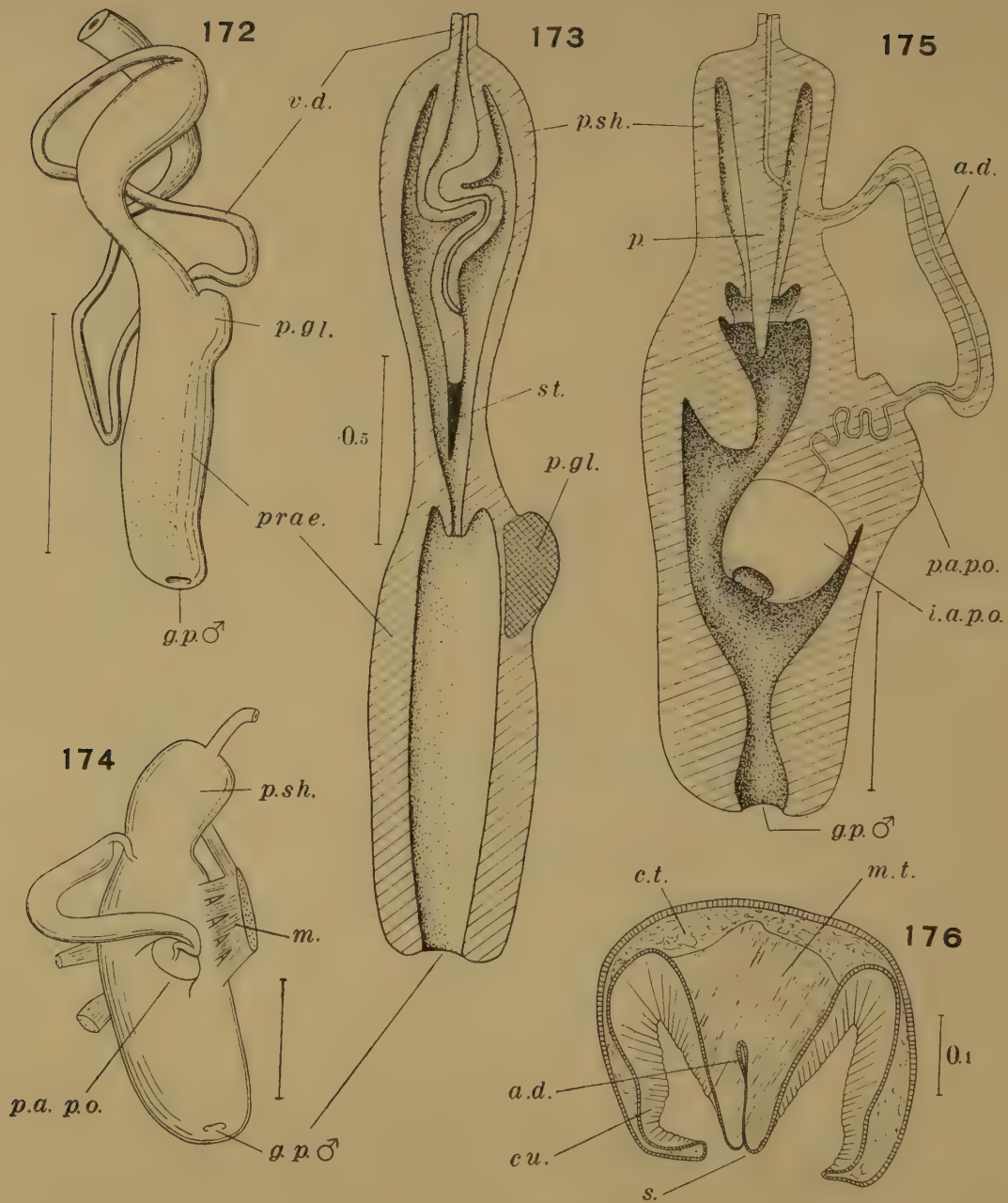
Fig. 172.—*Anisus sarasinorum* (Bollinger). Male copulatory organ.

Fig. 173.—Same species. Longitudinally sectioned male copulatory organ.

Fig. 174.—*Parapholyx effusa* (Lea). Male copulatory organ.

Fig. 175.—Same species. Longitudinally sectioned male copulatory organ. The tip of the accessory praeputial organ is left intact.

Fig. 176.—Same species. Section through the tip of the accessory praeputial organ. Semi-schematic.
(Key to lettering, p. 542)

Trochorbis Benson, 1855.

No material available.

Discoidal shell. The body whorl embraces almost the whole shell leaving only a very small umbilicus. Internal lamellae occur. Most authors have placed *T. trochoideus* Benson, the type species of the monotypic genus, in *Segmentina*. Conchologically it is still more similar to *Polypylis*. The morphology of the animal is completely unknown.

Tropicorbis Pilsbry & Brown, 1914.

Material. *T. canonicus* (Cousin) from Lago Langui, Peru (Coll. Percy Sladen Trust Exped. to Lake Titicaca 1937); *ibid.* from Lago de Junín and from the neighbourhood of Lake Titicaca (Coll. H. Macedo); *T. pallidus* Adams from a number of localities in Venezuela (Coll. by the author Febr.-April 1953).

Morphology. The shell is discoidal. The pallial opening and its appendages are similar to the corresponding structures in e.g. *Australorbis*. In some forms, however, the mantle lobe is almost non-existent (fig. 167). There is no renal ridge but dorsal and rectal ridges are present. The latter sometimes has transverse, vascularized folds. The jaw has no vertical bars. The cylindrical salivary glands are connected posteriorly.

The marginals of the radula (fig. 177 *m*) are of the long type with cusps also along the lateral edge.

The male copulatory organ (figs. 166, 169, 170) is simple. The penis is long and slender and has a wide sinus separating the central and peripheral parts of its tissue (fig. 171). A small sarcobelum and a somewhat folded velum are present at the junction between the penis sheath and the praeputium. There are one or two muscular pillars in the latter. The prostate (fig. 168) has numerous branched diverticula arising from a swollen portion of vas deferens. There is usually more than one diverticulum emerging from a cross-section of the duct.

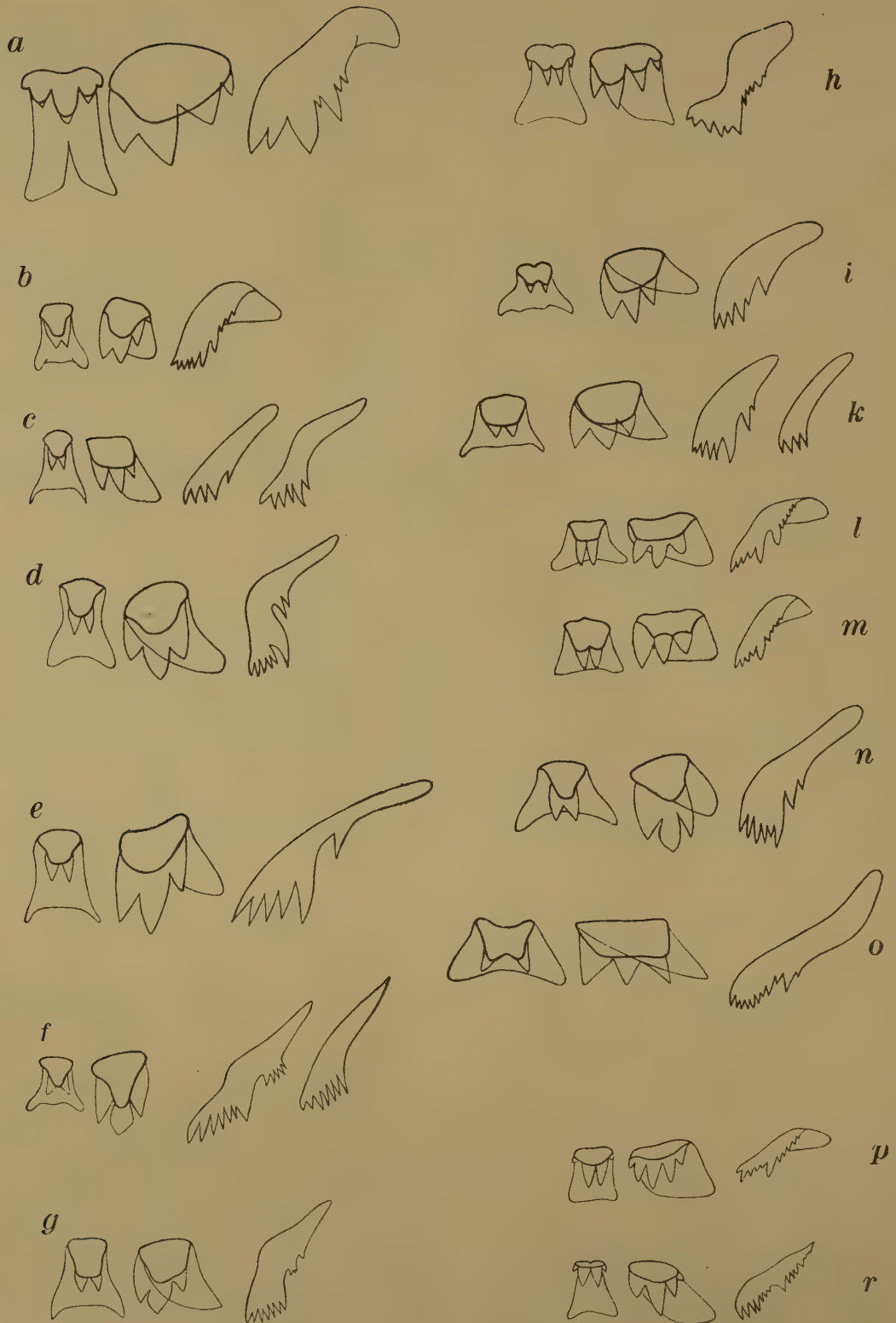
Remarks. There is no separate prostate duct in *Tropicorbis* as stated by Baker (1945).

COMPARATIVE MORPHOLOGY AND PHYLOGENY OF THE PLANORBIDAE.

The main branches and their relationships.

The genus *Plesiophysa* cannot be placed in any family but the Planorbidae (Hubendick, 1949). As a planorbid, however, it is very aberrant. The well-developed gill is situated in front of the anal pore instead of behind it. This indicates that the gill is probably homologous with the mantle lobe. If this is true *Plesiophysa* lacks a structure corresponding to the pseudobranch in other planorbids. The absence of this feature has to be regarded probably as a primitive condition. Other primitive features are the sinistral shell with a spire and the thick, lobed salivary glands which are not connected posteriorly. These and other peculiarities which characterize *Plesiophysa* represent an evolution in an aberrant direction. The probable transformation of the mantle lobe into a gill is mentioned above. Other characteristics of this type are the shape of the centrals and inner laterals of the radula, the exceptionally long ureter and the peculiar structure of the

Fig. 177.



shell material. To the same group of characteristics the flagellum and the praeputial gland probably belong. The former might be suspected to be homologous with the flagellum of *Segmentina* and related forms although that of *Plesiophysa* consists of a number of entangled, blind-ending ducts. The wide phylogenetic separation of *Plesiophysa* from other Planorbidae, indicated by a number of features, suggests, however, that there is no homology between the flagellum of *Plesiophysa* and other planorbids, e.g. *Segmentina*. The praeputial gland of *Plesiophysa* is most likely a new formation in this group. It is hardly probable that the similarly placed gland in *Physa* is homologous. On the whole the family Physidae is well defined from other Basommatophora. The praeputial gland in Physidae is most probably a development within the family. Further, the praeputial gland of *Plesiophysa* is morphologically quite different from that in Physidae. The praeputial gland in *Anisus sarasinorum* is much more similar to that in the Physidae but the homology of the glands in these groups is hardly possible.

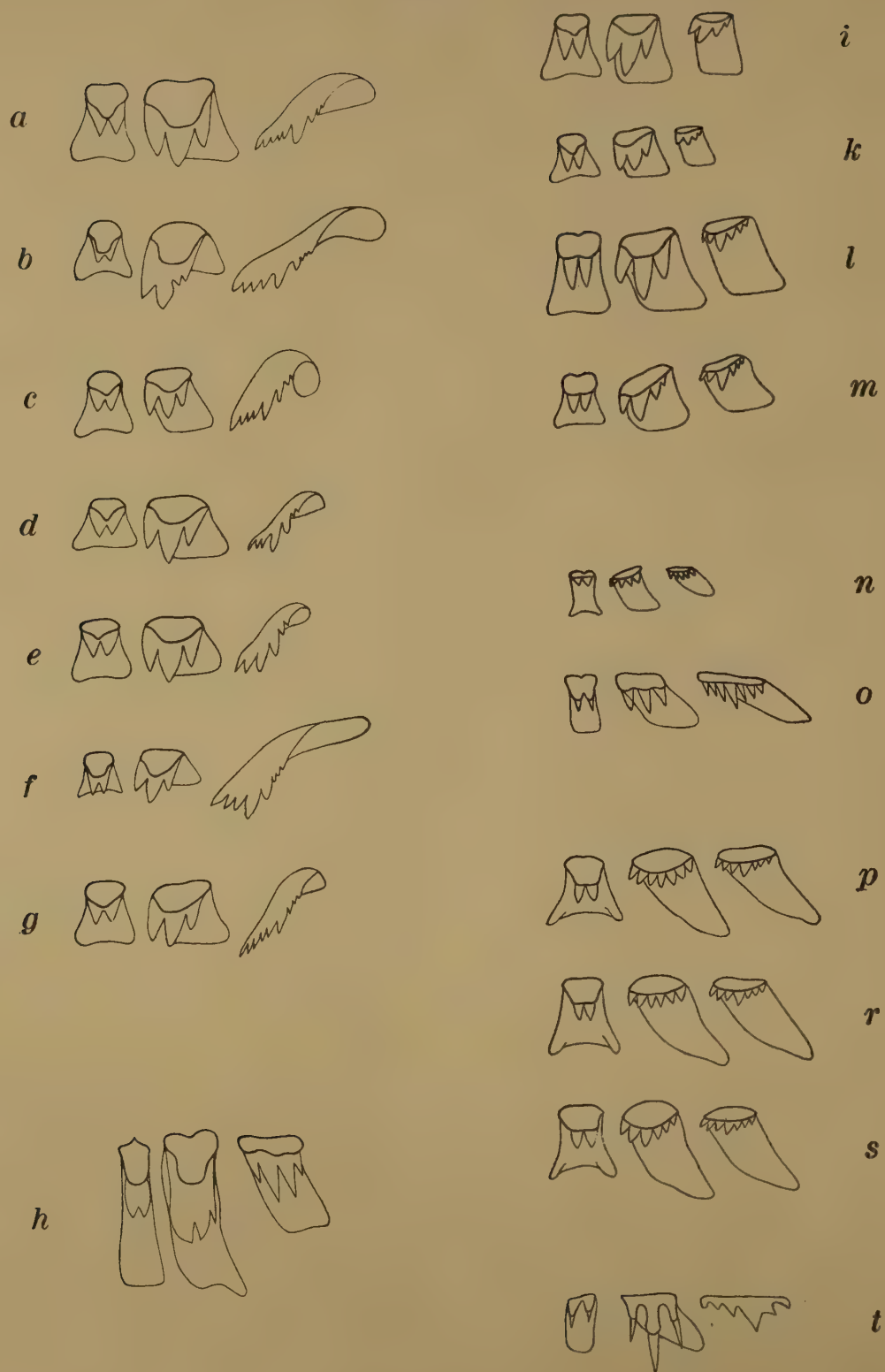
Camptoceras is another aberrant genus in the Planorbidae. It shows some conchological resemblance to *Plesiophysa*. *Camptoceras* also has an accessory praeputial organ though it does not seem to be glandular. A structure similar to the praeputial organ in *Camptoceras* is not known in any other planorbid. There are, however, some similarities between *Camptoceras* and *Plesiophysa* apart from the characteristics of the shell. *Camptoceras* has one big flap below the mantle pore. The extension and position of this flap and the gill in *Plesiophysa* are similar though their forms are different. Further similarities between *Plesiophysa* and *Camptoceras* are to be found in the salivary glands and in the kidney. A close relationship between the two genera is contradicted by the absence of a flagellum in *Camptoceras*, the form of the prostate, probably also the structures in the praeputium mentioned above, and, above all, by the type of central teeth in the radula. The form of these in the radula in *Camptoceras* is identical with those of the radula in *Drepanotrema* and *Fossulorbis*. There may be a close relationship between these three groups though some features contradict it. It is impossible to draw a definite conclusion as to the taxonomic position of *Camptoceras*. In this connection it is important only to state that *Camptoceras* does not fit in smoothly in the Plesiophysinae and that it belongs rather to the Planorbinae though its position within this subfamily is obscure.

The remaining planorbids can be divided into two groups (Hubendick, 1948 a). The one comprising *Bulinus*, *Physopsis* and *Indoplanorbis* (i.e. the Bulininae)

Fig. 177.—Central, first lateral and one or two marginal teeth from the radula of the following species. (The radulae are reproduced in the same order of size but in different magnification in order to facilitate comparison between radulae of different size.)

a. *Plesiophysa ornata* Haas; b. *Indoplanorbis exustus* (Deshayes); c. *Bulinus senegalensis* Müller; d. *Physopsis africanus* Krauss; e. *Amerianna leopoldi* Dupuis; f. *Miratesta celebensis* Sarasin & Sarasin; g. *Physastra badae* (Bollinger); h. *Camptoceras hirasei* Walker; i. *Biomphalaria smithi* Preston; k. *Afroplanorbis pfeifferi* (Krauss); l. *Australorbis glabratus* (Say); m. *Tropicorbis havanensis* (Pfeiffer); n. *Taphius montanus* (d'Orb.); o. *Platytaphius heteropleurus* (Pilsbry & Vanatta); p. *Drepanotrema anatinum* (d'Orb.); r. *Fossulorbis cultratum* (d'Orb.). (b, l and m redrawn from Baker 1945.)

Fig. 178.



is characterized by the presence of an ultra-penis, and the other consisting of the rest of the planorbids (i.e. the Planorbinae) is characterized by the presence of an ordinary penis. This difference between the two groups is important and confirms a true phylogenetical separation of the groups.

Except for *Plesiophysa* the radula shows two distinct main types in the family. The difference relates to the marginals. The one has the long, oblique type of marginals with cusps not only on the posterior end of the tooth but also along its lateral margin. The other type is shorter, comparatively symmetrical and without cusps along the lateral edge. The latter occurs exclusively in the Planorbinae and the former or oblique type, on the contrary, characterizes all the Bulininae as well as several groups of Planorbinae. This distinct division of the radula into two types is undoubtedly important from a comparative morphological point of view. It could indicate that Bulininae is no natural unit but related to the Planorbinae, with oblique marginals. These together could be separated from the remaining Planorbinae, i.e. those characterized by short marginals. This interpretation is hardly correct, however, because the oblique type of marginals is the original or primitive condition in the Planorbidae. The same type of marginals is present in the Lymnaeidae and are retained even in Ancyliidae. The occurrence of the oblique marginal type does not indicate any step of evolution. The presence of oblique marginals in different planorbid groups can never be evidence of a close relationship between these groups if other characters contradict it. The oblique marginals have simply been retained in the Bulininae and in some Planorbinae. Other Planorbinae have, however, evolved the other type of marginals.

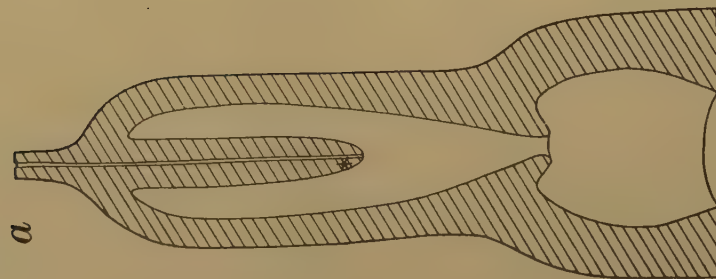
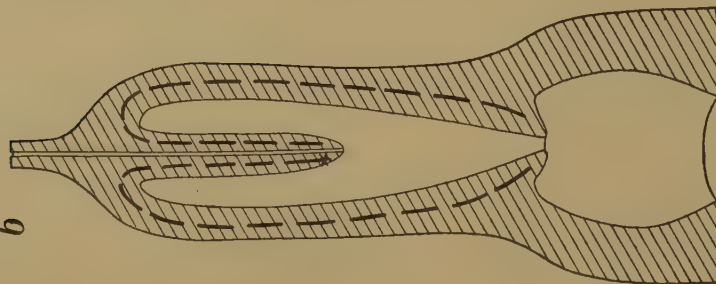
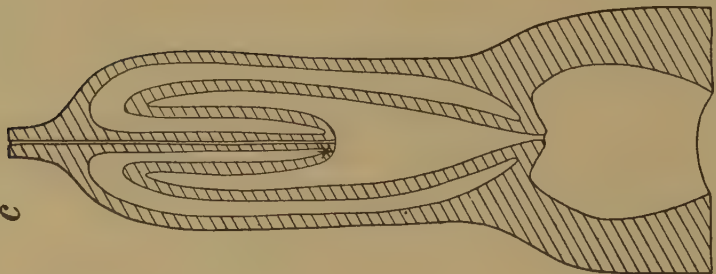
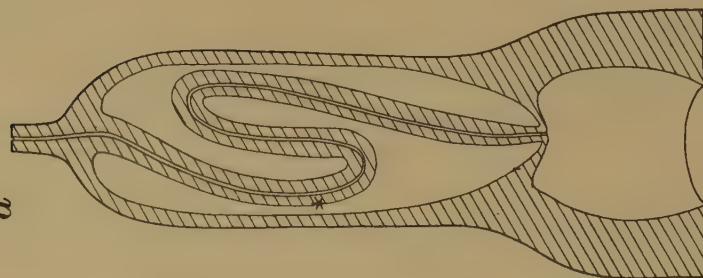
Of course it would be possible to reverse the arguments and say that the ordinary type of penis is an original or primitive feature in the Planorbidae and that the ultra-penis (cf. p. 497) is a secondary specialization within the family. Then we have to evaluate the importance of the characters themselves. The difference in the marginals of the radula is a simple step of evolution, probable without any considerable functional importance. The difference in the male copulatory organ, on the contrary, is the result of a comprehensive evolution which has caused considerable functional changes of different parts of the male organ. It can hardly have been accomplished by only one step of evolution. The evolution of the ultra-penis must have been regulated by natural selection in a much more intricate way than the evolution of the short type of marginals in the radula. Consequently, the structure of the male organ must be attributed with more evidence than the radula when used as a basis for phylogenetic conclusions in the Planorbidae.

Fig. 178.—Same as in fig. 177 from the following species:—

a. *Planorbarius corneus* (L.); b. *Helisoma anceps* (Menke); c. *Planorbula jenksi* (Carpenter); d. *Promenetus exacuous* (Say); e. *Menetus cooperi* Baker; f. *Carinifex ponsonbyi* Smith; g. *Parapholyx effusa* (Lea); h. *Choanomphalus amauronius* (Bourg.); i. *Planorbis planorbis* (L.); k. *Anisus spirorbis* (L.); l. *Gyraulus albus* (Müller); m. *Armiger* "imbricatus" (Müller); n. *Hippeutis complanatus* (L.); o. *Helicorbis mearnsi* (Bartsch); p. *Segmentina nitida* (Müller); r. *Polypylis calathus* (Benson); s. *Intha capitis* Annandale; t. *Acrorbis petricola* Odhner. (a–g, i–m and p–s redrawn from Baker 1945.)

Figs. 179-180.

179

a*b**c**d*

180

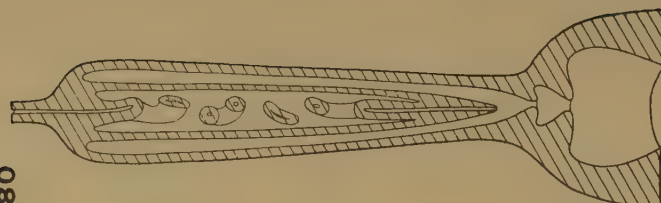


Fig. 179.—Diagram showing the evolution of the ultra-penis. The asterisks indicate a corresponding spot in the various states (see the text pp. 521-522).

Fig. 180.—Longitudinal section through the upper part of the male copulatory organ in *Biomphalaria* showing the sinus in the penis. (Hatched areas indicate cut surfaces.)

There are two differences between the male copulatory organ of the Bulinae and other Planorbidae. In the Bulinae the real penis of other Planorbidae is absent but a special ultra-penis is present. The Bulinae must almost of necessity have evolved from forms with a real penis. If we presume that copulation is of vital importance in these hermaphroditic snails also, the evolution of the ultra-penis cannot have been preceded by the disappearance of the ordinary penis. The copulatory organ must have been capable of acting through the whole process of evolution. If, on the other hand, copulation is not of vital importance, it is hard to understand how this evolution has actually taken place. It is most likely, that the ordinary penis has become transformed into the ultra-penis.

Fig. 181.

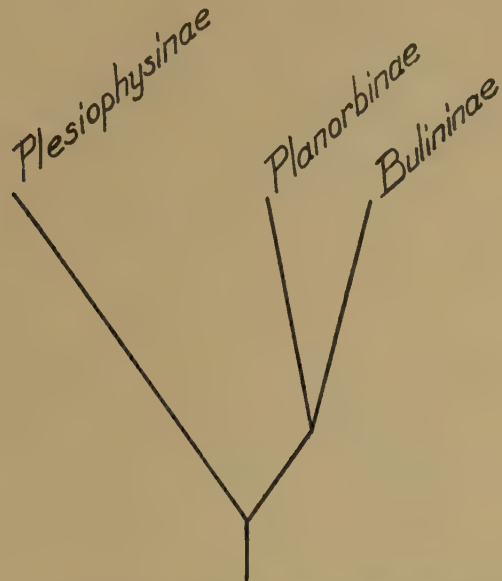


Diagram showing the most probable relationships between the main branches of Planorbidae, i.e. the subfamilies.

The transformation of an ordinary penis into a ultra-penis, or rather into part of an ultra-penis, can be explained in the following way. A slit develops in the tissue of the penis separating a central portion, surrounding vas deferens and a peripheral portion. At the tip of the penis the two layers are still connected. Such a condition is present in a few Planorbidae (*cf.* figs. 30, 171, 180) and also in many Lymnaeidae. The slit between the layers is sometimes wide, allowing the inner portion of the penis to coil within the slit. The evolution of an ultra-penis requires some further changes in the copulatory organ. The upper end of the slit becomes extended. It turns and penetrates down through the wall of the penis sheath and ends close to the place where the penis sheath merges into the praeputium. The next step in the evolution of the ultra-penis is that the peripheral layer of the penis and the central layer of the penis sheath wall turn inside out, forming an extension of the central portion of the original penis. This can happen through a proportionately faster growth of the peripheral layer of the penis sheath (future ultra-penis sheath). The other end of the extension remains connected with the peripheral portion of the penis sheath wall where it joins the upper end of

the praeputium. The peripheral epithelium of the original penis has become inner epithelium of the middle portion of the extended vas deferens in the ultra-penis. The epithelium of the penis sheath wall forms the epithelium of the distal portion of the extended vas deferens in the ultra-penis. All the changes and specializations in the histological structure of the ultra-penis constitute probably the last step in its evolution. And these changes make it impossible to recognize the original tissues in the three different parts of the ultra-penis (*cf.* figs. 107–114).

The formation of a slit in the penis in some Planorbinae which has actually taken place must be a parallel phenomenon. The discoidal forms in which such a slit is present can hardly be ancestors of the Bulininae (*cf.* below p. 524). In the physoid forms of Planorbidae no penis slit has been observed.

Larambergue (1939 *a*, p. 106) suggests putting *Bulinus* and *Indoplanorbis* in a distinct family, the Bulinidae. Except for the male copulatory organ, however, there are no important morphological differences between *Bulinus* and *Indoplanorbis* on the one side and the Planorbinae on the other. A distinction into subfamilies seems to correspond better to the natural conditions.

On the basis of comparative morphology and of the probable phylogeny, the family Planorbidae should consist of three subfamilies, viz. the aberrant Plesiophysinae and the comparatively closely related Bulininae and Planorbinae.

The subfamily Bulininae.

Bulinus, *Physopsis* and *Indoplanorbis* are provided with an ultra-penis and so belong to Bulininae. *Indoplanorbis* differs from the other genera in having a discoidal shell. This has almost certainly evolved within the subfamily from the physoid shell type still remaining in the other genera. This evolution is independent of similar parallel phenomena in the subfamily Planorbinae.

Apart from the difference in shell form there are a few small morphological differences between *Indoplanorbis* on one side and *Bulinus* and *Physopsis* on the other. There are two rectal ridges in *Indoplanorbis*. One of them is certainly a new development without a parallel in any other planorbid group. The salivary glands in *Indoplanorbis* are partly lobed but are tubular throughout in *Bulinus* and *Physopsis*.

The difference between *Indoplanorbis* and the two other groups indicate a progressive evolutionary step in *Indoplanorbis*. Parallel with the evolution of the body form in general, a further concentration of the central nervous system could be expected in *Indoplanorbis*. There is, in fact, a general tendency in Planorbidae, as in the Basommatophora as a whole, to concentrate the nervous system. The central nervous system of *Indoplanorbis* does not, however, show any more concentration than can be found in the corresponding structure in *Bulinus* and *Physopsis* (*cf.* figs. 182, 183).

Bulinus and *Physopsis* are morphologically very similar and closely related. One anatomical difference only is known. There is no renal ridge in *Bulinus* but it is present in *Physopsis*. This can hardly be considered as a very important difference as both conditions are known from one and the same species of another planorbid group. Conchologically *Bulinus* is characterized usually by a continuous

columella which is not truncated. The nuclear whorls are usually provided with striae. In *Physopsis* the columella is generally truncated. The nuclear whorls are usually not striated but have small dots spirally arranged. Sometimes, however, the correlation between these characters does not hold good. All this means that *Bulinus* and *Physopsis* should be regarded as subgenera of one genus (*Bulinus*) rather than as distinct genera.

Figs. 182-183.



The central nervous system.

Fig. 182.—*Bulinus natalensis* (Küster).

Fig. 183.—*Indoplanorbis exustus* (Deshayes). Buccal ganglia not included. (For explanation of the figures see under figs. 201-208, p. 531.)

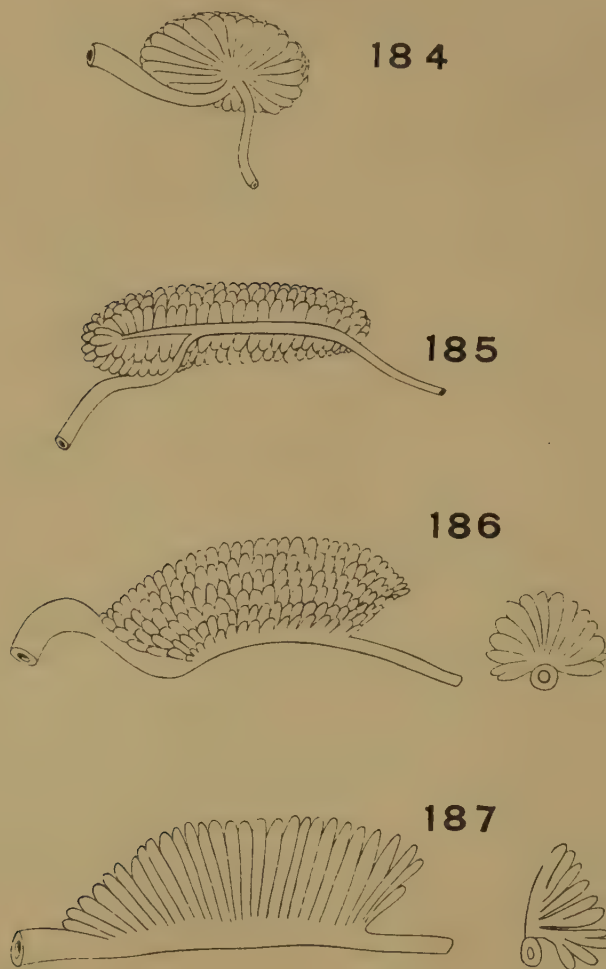
In a previous paper (Hubendick, 1948 a) *Physopsis* was treated as a synonym of *Bulinus*. *Pyrgophysa*, on the other hand, was kept as a valid group on account of some anatomical features. New and better preserved material of a species belonging to this group has shown that there is no significant difference between *Pyrgophysa* and *Bulinus*. All forms with a physoid or spired shell in *Bulininae* have to be classified as *Bulinus*; this genus, together with *Indoplanorbis*, are therefore the only remaining genera of this subfamily.

The main branches of the subfamily Planorbinae.

It has been noted above that the family Planorbidae is morphologically heterogeneous; this applies also to the Planorbinae. Different branches have evolved along more or less divergent lines and the ends of the branches, represented by recent genera, are generally distinctly separated from each other. They are separated by differences in various structures. Sometimes, however, these differences contradict each other in certain characteristics, making the whole picture confusing. The importance of the various features had to be assessed on a comparative basis. Characters forming an evolutionary trend are more easily interpreted than others.

The Planorbidae must have evolved from gastropods with a spired, sinistral shell. Such a shell is, consequently, an original or primitive family condition. A discoidal and a pseudo-dextral shell represent further evolutionary stages or more specialized structures. In a corresponding way a moderately concentrated central nervous system is to be regarded as more primitive than a more concentrated

Figs. 184–187.



The prostate of the following species (based on figures in Baker 1945):—

Fig. 184.—*Helisoma tenue* (Philippi).

Fig. 185.—*Helisoma traski* (Lea).

Fig. 186.—*Helisoma corpulentum* (Say). Cross-section to the left.

Fig. 187.—*Planorbula armigera* (Say). Cross-section to the left.

system, the latter being a more specialized stage within the family. The variation in the central nervous system is, however, very limited in Planorbidae (see figs. 201–208). Other structures do not show real trends though they appear in different forms in the various groups. In some instances, however, it is possible

to deduce which form represents the original stage and which form represents the specialized stage. If a structure appears in the same form in all three subfamilies as well as in another form in one of them, this last form must be considered as probably lately evolved. The same can be true also if the original stage is present in the Bulininae and the Planorbinae only, because *Plesiophysa*, the single recent representative of Plesiophysinae, is morphologically aberrant through divergent evolution. From this type of reasoning it can be concluded that the following features represent the original stage in Planorbidae: the presence of pallial ridges, long marginals with both posterior and lateral cusps, a terminal pore on the penis, no flagellum or other appendages on the copulatory organ, and a simple prostate.

Concerning the mantle appendages it can be concluded that a simple flap is the most primitive arrangement. The folded pseudobranch has certainly evolved within the family, possibly more than once. Reductions have occurred leading to a deceptive resemblance between the highest evolutionary stage and the original stage in certain respects. This is evident from a comparison with other characters.

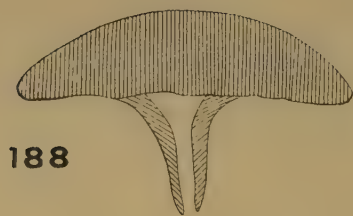
With the exception of the branched gill and the well-developed prostate the structure of *Amerianna* corresponds well to that of a primitive planorbid. The group is sharply defined from all other planorbids and constitutes a tribe* of its own. The structure of the prostate hardly contradicts the general primitive condition of *Amerianna*. The prostate is evidently an easily changeable organ in the family. Within the genus *Helisoma* for instance there are different types of prostate, some of which must have evolved within the genus (figs. 184–187). Likewise in the tribe comprising *Helisoma* and some more genera the evolution of the prostata shows a distinct trend resulting in a structure similar to the prostate in *Amerianna*. Obviously this special type of prostate has evolved independently more than once in the Planorbinae. Most probably the same is true for some other types of prostate.

Physastra and *Miratesta* have a type of prostate similar to but not identical with that of *Amerianna*. The ancestral shell form, i.e. the sinistral, spired type of shell, is retained in these genera as it is in *Amerianna*. In both *Amerianna* and *Physastra*, but not in *Miratesta*, the dorsal part of the jaw can be composed of vertical bars. This is probably of little comparative importance as this special structure in the dorsal part of the jaw seems to have evolved independently within the two genera. Species with a homogenous or almost homogenous dorsal part of the jaw occur in both genera (figs. 188, 195). In *Physastra* the species can even be arranged as a typological series connecting a homogenous jaw with a jaw composed of strong vertical bars (figs. 188–193). In *Planorbis* (fig. 197) and related genera also the jaw is composed of vertical bars or more correctly of plates. The latter is probably still another recently evolved character. Here the whole jaw as well as its lateral parts consists of vertical plates. In addition, the jaw differs somewhat from that of other groups in having a more continuous connection between the dorsal and the lateral parts.

Physastra and *Miratesta* differ from *Amerianna* in having a lateral penis pore.

* Here in this paper *tribe* is used as indicating an evolutionary line rather than a strict nomenclatorial group.

Figs. 188-199.



188



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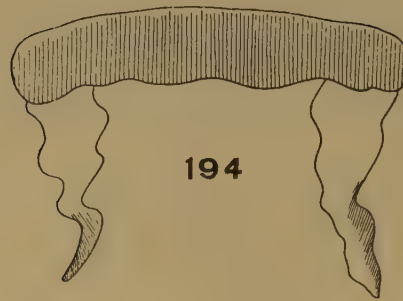
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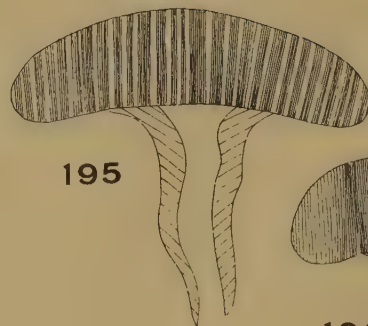
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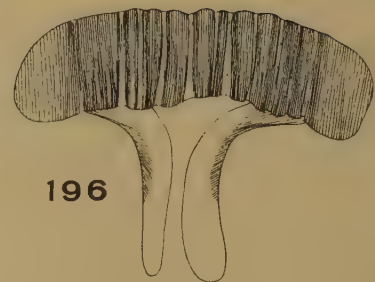
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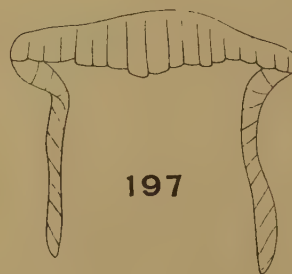
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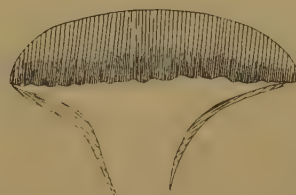
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199

In *Physastra* a stylet is also present. A similar arrangement, a lateral penis pore and a stylet is present also in most of the genera related to *Planorbis*. These two characteristics in the different groups may have a common origin. Such a common origin means that *Physastra* together with *Miratesta* and *Planorbis* with related genera have branched off together from the line which gave rise to *Amerianna*. This is an argument in favour of the independant evolution of the well-developed prostate glands in *Amerianna* and *Physastra*. Although, on the one hand, *Physastra* together with *Miratesta*, and on the other, *Planorbis* together with related genera, have evolved in step for a little way, the latter group is well separated from the former through the short marginals in the radula.

In *Miratesta* there is no stylet but a lateral pore. It is most likely that the evolution of a lateral pore is combined with the evolution of a stylet. The lateral pore in *Miratesta* therefore indicates that a reduction of the stylet has probably taken place. The lateral pore is to be considered as a vestigial character, which does not contradict the close relationship between *Miratesta* and *Physastra*. These two genera have most probably a common origin and form a distinct tribe within the subfamily. In both genera certain special features have evolved. In *Physastra* there is a peculiar, muscular flagellum without anything corresponding to it in the whole family. In *Miratesta* the peculiar shape and structure of the shell, the peculiar form of penis and spermatheca and radular marginals with two well separated groups of cusps have evolved.

All the Planorbinae can be divided into two groups with reference to the radula. The one group is characterized by long marginals with cusps along the posterior and lateral edges. The other group is characterized by short marginals with cusps along the posterior edge only. This division is not always supported by the characteristics of the copulatory system. There are, for instance, some genera in both groups (classified according to the marginals) with an accessory duct outside the praeputium. These or other features in the copulatory organs may, however, be of less comparative value than those of the radula. A particular change in the radula may be due to a single mutation but the selection value of such a change can hardly be great. With all probability the selection value of a definite change in the copulatory system can be expected to be considerably greater because it is of more functional significance. Further, within the Planorbidae the radula

Frontal view of the jaw from the following species :—

- Fig. 188.—*Physastra* sp. from South Australia.
- Fig. 189.—*Physastra sarasinorum* (Bollinger).
- Fig. 190.—*Physastra ovalinus* (Martens).
- Fig. 191.—*Physastra gibbosus* (Gould).
- Fig. 192.—*Physastra sumatranus* (Martens).
- Fig. 193.—*Physastra minahassae* (Martens).
- Fig. 194.—*Miratesta celebensis* Sarasin & Sarasin.
- Fig. 195.—*Amerianna leopoldi* (Dupuis).
- Fig. 196.—*Amerianna buruanus* (Bentham Jutting).
- Fig. 197.—*Planorbis planorbis* (L.).
- Fig. 198.—*Physopsis africanus* (Krauss).
- Fig. 199.—*Bulinus inflatus* (Adams & Angas).

shows only a few different types but the copulatory organs are very variable. This makes one inclined to consider the radula as the more important comparative feature. It seems more probable that certain characters in the copulatory organs than certain characters in the radula have evolved parallelly at different instances. The consequence of all this is that the subfamily Planorbinae should be divided into two main branches according to the form of the marginals in the radula or rather that all genera with short marginals represent one main branch within the subfamily.

Fig. 200.

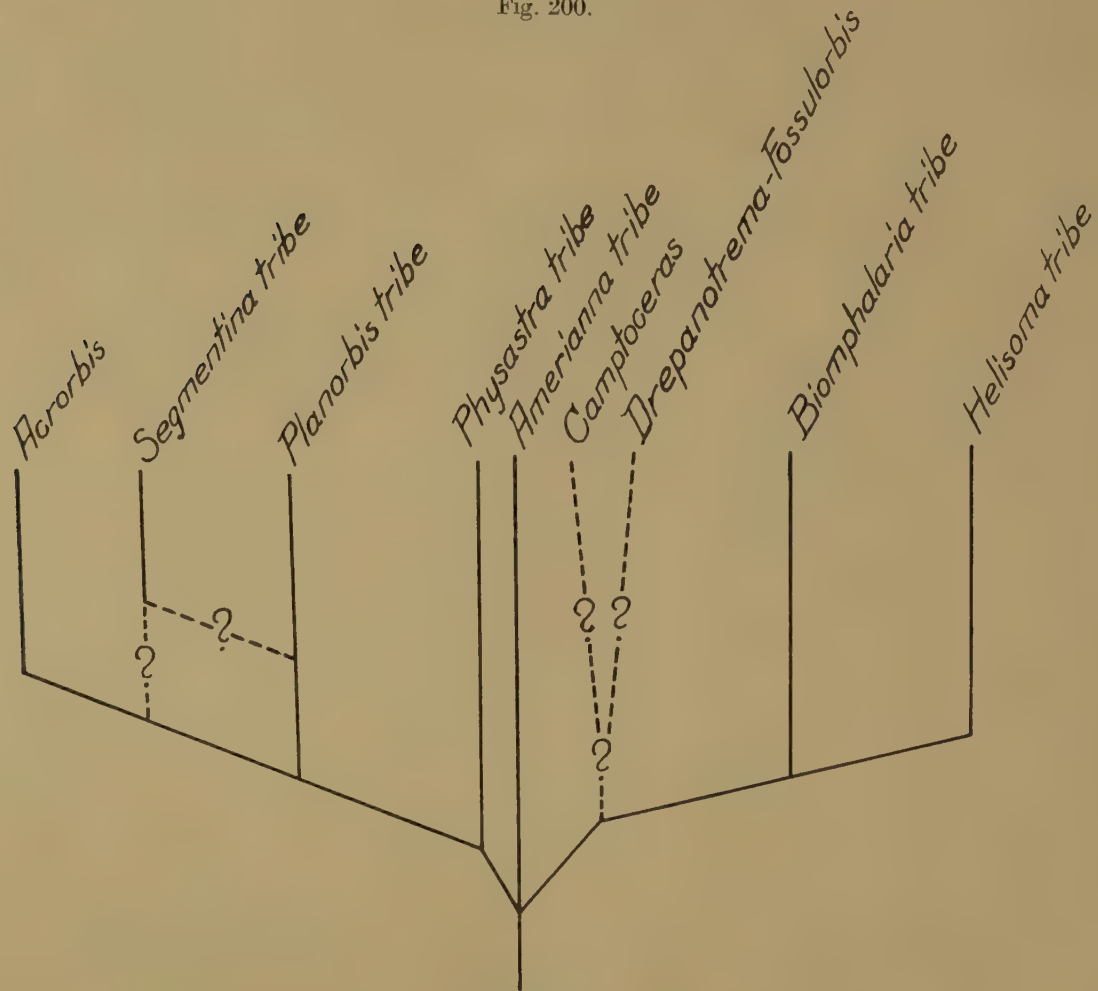


Diagram showing the most probable relationships between the groups within the subfamily Planorbinae.

To the main branch with short marginals belong *Planorbis* with its related genera (i.e. *Anisus*, *Gyraulus*, *Armiger* and *Choanomphalus*) which have already been mentioned. These genera, possibly with the exception of *Choanomphalus*, are characterized by the presence of a separate prostatic duct. In *Planorbis* the stylet is lacking and the penis pore is terminal. This could be due to a reduction within the tribe. It seems, however, more probable that the absence of a stylet in *Planorbis* is a primitive condition and that the stylet has evolved

within the *Planorbis* tribe. In this tribe the stylet consists of a thin chitinous sheath of varying form, abruptly delimited from the non-chitinated part of the penis. In *Physastra*, on the contrary, the soft part of the penis merges gradually into the solid stylet which becomes more and more dense in a distal direction. Consequently, it seems likely that the stylet in the *Physastra* tribe and the *Planorbis* tribe are not homologous but have evolved parallelly and independently. This conclusion is, however, not supported by the presence of a stylet, or a cuticular cover at least, on the tip of the penis in *Polypylis*.

In contradistinction to the *Planorbis* tribe, where no flagellum occurs, the tribe consisting of *Segmentina* and related genera, i.e. *Polypylis*, *Intha*, *Pingiella*, *Hippeutis* and *Helicorbis*, are characterized by two flagella. As in the *Planorbis* tribe short marginals and a separate prostatic duct are also present. The flagella in this tribe are glandular and quite different from that in *Physastra*. Some peculiar specializations in the male copulatory organ occur in the *Segmentina* tribe.

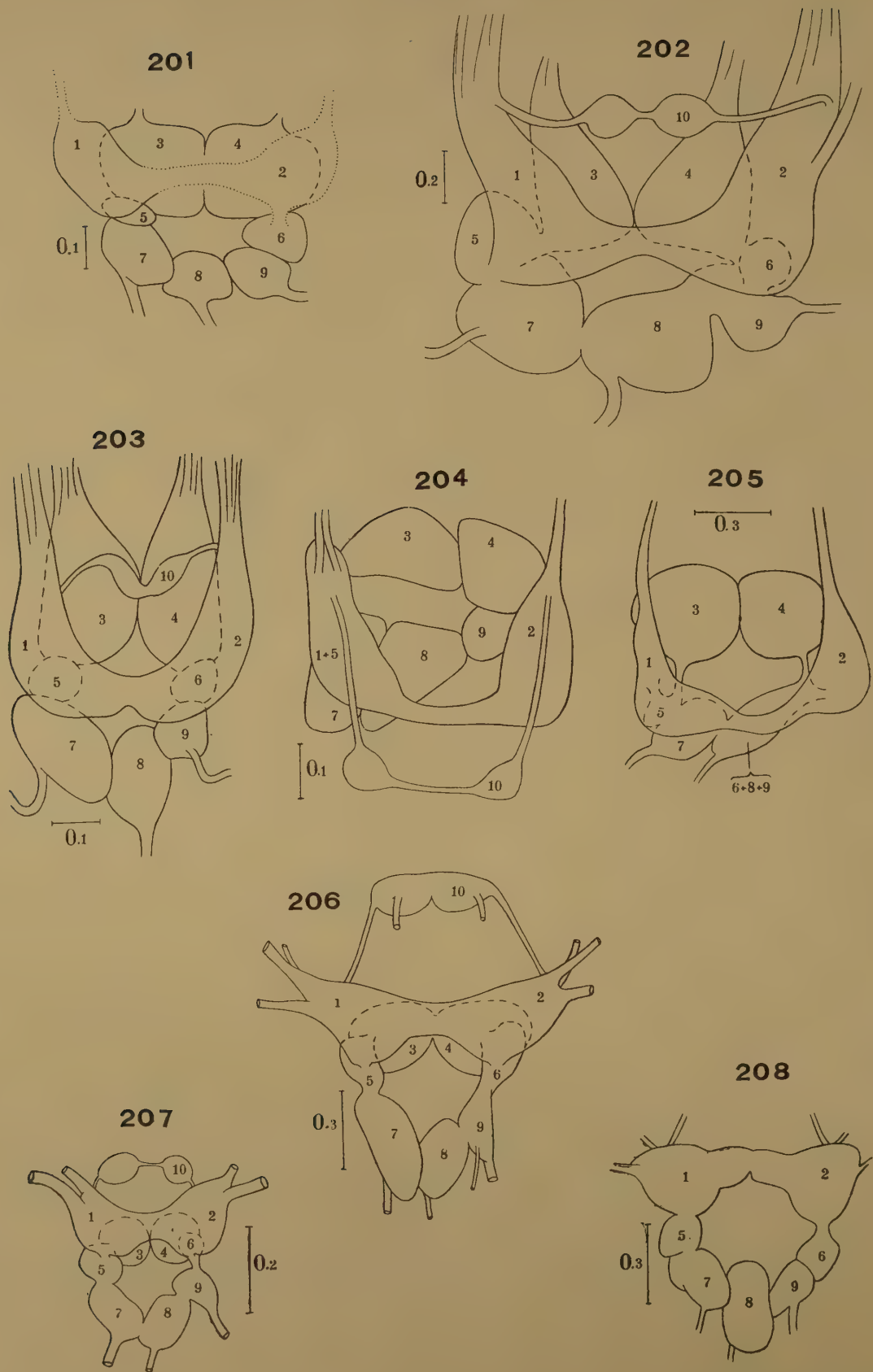
Another genus, *Acrorbis*, has short marginals. This genus also has two flagella though there is no connexion between their lumina and the penis sheath. Conchologically *Acrorbis* represents the highest evolution in the Planorbidae as it is pseudo-dextral (see p. 524). However, its prostate seems to have a more primitive structure than that of the *Segmentina* and *Planorbis* tribes. It seems to have no separate prostate duct but has a number of diverticula arising directly from vas deferens. If the primitive type of prostate is really retained in *Acrorbis* there are two possible consequences. The first is that the flagella of *Acrorbis* are not genetically identical with those in the *Segmentina* tribe but the prostatic duct may have a common origin in the *Segmentina* and *Planorbis* tribes. The second is that the flagella in *Acrorbis* and the *Segmentina* tribe have a common origin and that the separate prostatic duct has evolved independently in the *Segmentina* and the *Planorbis* tribes. It seems not possible at present to reach a definite conclusion as to which view is correct.

The second main branch of Planorbinae, the one with long marginals, consists, if *Amerianna*, *Physastra* and *Miratesta* are disregarded, of three tribes though the status of one of them is somewhat doubtful. The genera *Biomphalaria*, *Afroplanorbis*, *Australorbis*, *Tropicorbis*, *Taphius* and *Platytaphius* are morphologically very similar. They have a more or less discoidal form and a simple copulatory organ without special features as well as a terminal penis pore. They have a comparatively simple prostate. Of the pallial ridges only the renal ridge is usually reduced. The jaw has no vertical bars. The whole internal morphology of the genera under consideration has a comparatively primitive appearance. Together they form a uniform tribe.

Another distinct tribe is formed by *Helisoma* and related genera, i.e. *Planorbarius*, *Promenetus*, *Menetus*, *Planorbula*, *Parapholys* and *Carinifex*. In addition to the more primitive long marginals and at least dorsal and rectal ridges, these genera are characterized by certain peculiar specializations in the male copulatory organ. The prostate also has undergone evolution. Sinistral, discoidal as well as pseudo-dextral shell types occur in the *Helisoma* tribe.

Another three more genera are provided with long marginals in the radula.

Figs. 201–208.



These genera are *Drepanotrema*, *Fossulorbis* and *Camptoceras*. All three are, further, characterized by quadricuspid centrals. In almost all other respects *Camptoceras* and the two other genera differ. It is doubtful whether there is a close relationship at all between *Camptoceras* and the other two genera. This problem and the taxonomical position of *Camptoceras* has already been discussed in connection with Plesiophysinae. The position of *Drepanotrema-Fossulorbis* too is doubtful. In these genera the male copulatory organ is simple with a terminal penis pore. There are, however, two flagella. In some species they are well developed, in others they show a trace of reduction, and in still others, they are almost completely reduced. The flagella are histologically similar to those in the *Segmentina* tribe. A common origin of the flagella in *Drepanotrema-Fossulorbis* and the *Segmentina* tribe is, however, contradicted by the different form of marginals in the two groups. The difference relating to the marginals in connexion with other features necessitates a wide systematic separation of the two groups. *Drepanotrema* and *Fossulorbis* may represent a tribe which has branched off from the evolutionary line leading to the *Biomphalaria* tribe and the *Helisoma* tribe.

The most probable relationships between the main groups of Planorbinae are presented diagrammatically in fig. 200.

The *Planorbis* tribe.

The *Planorbis* tribe comprises the genera *Planorbis*, *Anisus*, *Gyraulus*, *Armiger* and *Choanomphalus*. As far as the mantle appendages and the pallial organs are concerned these genera form a uniform group. Only in *Planorbis* does the male copulatory organ have a terminal penis pore without a stylet. If the lateral pore in *Physastra* and *Miratesta* and the stylet in *Physastra* have a common origin with corresponding features in the *Planorbis* tribe, the terminal pore and absence of stylet in *Planorbis* must be secondary. If, on the other hand, the characters under consideration have evolved independently in the respective groups, the terminal pore and absence of stylet in *Planorbis* is most probably primitive.

Anisus, *Gyraulus* and *Armiger* are anatomically very closely related. It is even doubtful if there is sufficient reason to retain separate genera. When more species have been anatomically examined the differences between the genera

Diagram of the central nervous system in the following species (buccal ganglia excluded in some of the figures) :—

Fig. 201.—*Amerianna pesigani* (Hubendick).

Fig. 202.—*Physastra* sp. from Tailem Bend, Murrey River, South Australia.

Fig. 203.—*Planorbis planorbis* (Linné).

Fig. 204.—*Choanomphalus amauronius* (Bourguignat).

Fig. 205.—*Camptoceras hirasei* Walker.

Fig. 206.—*Australorbis glabratus* (Say).

Fig. 207.—*Drepanotrema aeruginosus* (Morelet).

Fig. 208.—*Helisoma wyldi* (Tristram).

1=left cerebral ganglion

2=right cerebral ganglion

3=left pedal ganglion

4=right pedal ganglion

5=left pleural ganglion

6=right pleural ganglion

7-9=visceral ganglia

10=right buccal ganglion

will probably be overlapped by variation within the genera. The examination of *Anisus sarasinorum* indicates such a possibility.

Choanomphalus is undoubtedly the most specialized member of the *Planorbis* tribe. Its shell is pseudo-dextral. The left pleural ganglion is probably not free (fig. 204). An accessory gland complex, with a pore just beside the male genital

Fig. 209.

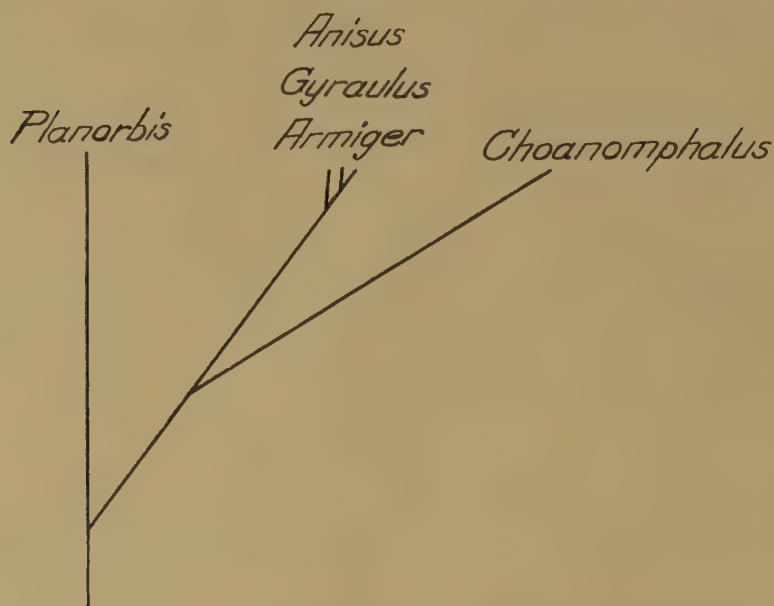


Diagram showing the most probable relationships between the genera of the *Planorbis* tribe.

pore, is present. A free prostate duct has not been observed, nor has the absence of such a duct been noticed. The author has not seen the whole prostate. Dybowski (1875), who figured a prostate without a free duct, can easily have overlooked it as he had certainly never considered the possibility of its existence.

I believe that the most probable relationships within the *Planorbis* tribe are as shown diagrammatically in fig. 209.

The *Segmentina* tribe.

The *Segmentina* tribe consists of the following genera: *Segmentina*, *Polypylis*, *Intha*, *Pingiella*, *Hippeutis* and *Helicorbis*. The first four genera form a unit characterized by a special type of radula (figs. 178 *p-s*) which does not occur in any other planorbids. *Helicorbis* shows a tendency to have the same characteristic. *Segmentina* and *Polypylis* are distinguished conchologically from the other genera by the presence of internal lamellae in the shell. *Polypylis*, *Helicorbis*, *Pingiella* and *Intha* have an accessory duct running from the proximal end of the praeputium to a praeputial organ, but *Segmentina* and *Hippeutis* have not. In *Hippeutis* the sperm duct has a terminal outlet. All the other genera have a more or less lateral outlet, or, at least, with a stylet or a papilla below the penis pore. *Hippeutis* has short flagella; all the other genera have long flagella. All these have a special structure in the praeputium. This structure is simpler in *Hippeutis* than

in the other genera. *Hippeutis* is obviously less specialized than all the others and taxonomically separated from them. The discovery that the various differences between these genera contradict each other renders attempts at classification very difficult. It follows, that in order to solve the relationships between these fairly closely-linked genera, there must be a proper assessment of the taxonomic importance of each feature which can be used for classification. An attempt, too, must be made to get some idea of their importance in phylogeny, in other words, are they primitive or vestigial, reduced, or that perhaps parallel evolution has been going on. Although in this tribe there is little chance of arriving at the right conclusion there are some aspects which can be discussed below.

The accessory praeputial organ with its accessory duct in *Helicorbis*, *Polypylis*, *Intha* and *Pingiella* is a very strange structure. It is not quite easy to understand its function and evolution. However, the purpose and evolution of the similar, but not identical, structure in the *Helisoma* tribe can be explained. But it cannot be presumed that the structure has the same function and a similar evolution in both instances. In *Segmentina* there is no accessory duct but a sort of accessory structure in the praeputium. This structure looks like a sucker and most probably it works as a hold-fast-organ during the copulation when the praeputium is turned inside out. The organ can easily be interpreted as having evolved from a muscular pillar. According to Baker (1945, Plate 8) a similar sucker-like organ is present in the praeputium of *Intha*, but there it is connected with the uppermost end of the praeputium through an accessory duct outside the male organ. Functionally the presence of such a duct can be explained as an improvement of the sucking mechanism. Its evolution is more difficult to explain. The condition in *Helicorbis umbilicalis* (fig. 75) may point in a special direction. The fact that parts of the accessory duct are enclosed within the wall of the praeputium may indicate that the duct was formed originally as a fold in the praeputial wall. However, in *Helicorbis umbilicalis* the accessory structure can hardly work as a sucker as the distal opening of the duct is extremely narrow if present at all. And the condition in this species can scarcely be regarded as a progressive evolutionary stage if it is not functional. An examination of more species may throw more light on the evolution of the accessory praeputial organ and the accessory duct of the *Segmentina* tribe.

The *Biomphalaria* tribe.

The *Biomphalaria* tribe includes the following genera: *Biomphalaria*, *Afroplanorbis*, *Australorbis*, *Tropicorbis*, *Taphius* and *Platytaaphius* and probably *Syrioplanorbis*. It is the most uniform tribe within Planorbinae and its representatives are the least specialized discoidal planorbids. The whole tribe is anatomically so homogenous that it is doubtful if the present separation into genera can be maintained. Neither the conchological nor the anatomical differences are really of generic value. The only obvious differences relate to the prostate, but these are superficial and the various types can easily be derived from the same general main type.

Watson (1954) has grouped together *Biomphalaria* (including also *Afroplanorbis*),

Australorbis and *Tropicorbis* as a subfamily called *Biomphalariinae*. Ranson (1953) has also made some contributions to our knowledge of the *Biomphalaria* tribe.

The *Helisoma* tribe.

The *Helisoma* tribe includes the following genera: *Helisoma*, *Planorbarius*, *Promenetus*, *Menetus*, *Planorbula*, *Parapholyx* and *Carinifex*. The combination of long marginals in the radula, lateral penis pore and absence of convoluted pseudobranch distinctly separate off the *Helisoma* tribe from other members of Planorbinae. Nevertheless there is a pronounced polymorphism within the tribe as far as the male copulatory organ is concerned.

Helisoma, *Parapholyx* and *Carinifex* have an accessory duct connecting the lumen of the penis sheath with that of the accessory praeputial organ. Such an organ, either with or without a lumen, is present also in the genera where an accessory duct is absent. The praeputial organ shows specialization in different directions in the various genera but a general evolutionary line can be traced with some degree of probability. This evolutionary line demonstrates the origin of the accessory duct in the tribe. Indirectly it may also explain the origin of the accessory duct which is present in some genera of the *Segmentina* tribe.

In *Planorbula* the dominating fold formation in the praeputium consists either of two closely adhering folds or of one fold which is secondarily cleft into two by a deep, narrow slit. In *Planorbarius* there is a similar structure which is provided with some special features, i.e. a T-shaped slit and two glandular ridges. In *Promenetus* the structure has increased in size and fills up almost the whole praeputium. The slit is more complex, being divided up into several branches. In *Menetus* the accessory praeputial structure is mainly similar to that of *Promenetus*. Its lumen is open proximally, i.e. towards the neighbourhood of the point where the penis sheath opens into the praeputium. If the middle portion of the slit in the praeputial organ becomes closed an accessory duct will be formed. One end of the duct will open distally on the accessory organ and the other end near the opening of the penis sheath. The whole duct will still be embedded in the praeputial wall or its derivatives. In *Parapholyx*, *Carinifex* and *Helisoma* a part of the duct runs outside the male organ, free from the praeputial wall. The evolution of this condition can be explained theoretically in the following way. The duct in the praeputial wall comes to lie close below the surface of the praeputium. By means of invaginations on the surface of the praeputium on either side of the duct, which finally meet below the duct, the latter becomes free; the length of the free portion will depend on the length and completeness of the original invagination. In other words the duct becomes cut off from the praeputial wall forming a free duct. In *Parapholyx*, *Carinifex* and *Helisoma* the upper end of the accessory duct reaches the penis sheath. The extension of the duct from the praeputium to the penis sheath can be explained in the same way as the formation of the lower part of the duct.

The various recent genera of the *Helisoma* tribe seem to correspond to different steps in an evolutionary series. This does not mean, however, that there must be a corresponding relationship between the genera; other features contradict it.

The various genera have merely retained different stages in the evolution of the accessory praeputial organ though they have undergone further evolution in other characteristics. At present it is hardly possible to put forward a real picture of the relationships between the genera of the *Helisoma* tribe.

SYSTEMATIC REMARKS.

The result of my investigations show that the classification of the family Planorbidae presented by Baker (1945) does not completely correspond to natural relationships. His classification comprises only part of what is dealt with here as the subfamily Planorbinae. His subfamilies correspond in the main to some of my tribes in the subfamily Planorbinae. At least one, possibly two, of Baker's subfamilies are not homogenous or monophyletic. The two other subfamilies of Baker seem to be artificially separated and together they correspond to my *Helisoma* tribe.

Baker's subfamily Planorbinae is heterogenous and consists of my *Planorbis* and *Biomphalaria* tribes. Baker's statement that his subfamily Planorbinae is characterized by the presence of a separate prostate duct is not true as far as members of my *Biomphalaria* tribe is concerned. In his subfamily Segmentininae Baker includes all the genera of my *Segmentina* tribe as well as *Acrorbis* and *Drepanotrema-Fossulorbis*. *Acrorbis* may form a natural unit together with the *Segmentina* tribe. The relationships of *Drepanotrema-Fossulorbis* is still not clear enough to allow a definite classification. Baker's subfamily Helisomatinae corresponds to part of my *Helisoma* tribe. The remaining genera of the *Helisoma* tribe, *Planorbula*, *Promenetus* and *Menetus*, are placed in a separate subfamily, Planorbulinae, by Baker. The separation of these two subfamilies is based on differences in arrangement of the diverticula in the prostate and the ovotestis. Such features can hardly be used for distinguishing subfamilies within Planorbidae, where a number of other, really important characters vary to a great extent. However, Baker referred to a third difference when separating his two subfamilies. He said that Helisomatinae are characterized by a "penial gland duct", i.e. an accessory duct, outside the praeputium and that the Planorbulinae are characterized by such a duct inside the praeputium. The last statement is due to a misinterpretation. There is no accessory duct at all in *Planorbula*, *Promenetus* and *Menetus* though a structure corresponding to the distal end of such a duct can be traced. *Planorbarius*, which has no accessory duct, has been placed in Helisomatinae by Baker, but it is now obvious that the recognition of groups corresponding to Baker's subfamilies Helisomatinae and Planorbulinae cannot be maintained.

It is still too early to undertake a critical revision of the validity of the various genera in Planorbidae. Genera which at present seem to be distinguished might be connected by intermediate forms when more species have been anatomically examined. In some cases, however, it is already apparent that a separation into genera cannot be maintained. In the subfamily Bulininae *Physopsis* and *Bulinus* are very closely related. Conchological and anatomical characters separate the groups but sometimes they contradict each other. It is better to regard the two groups as two subgenera of the genus *Bulinus* than as two genera.

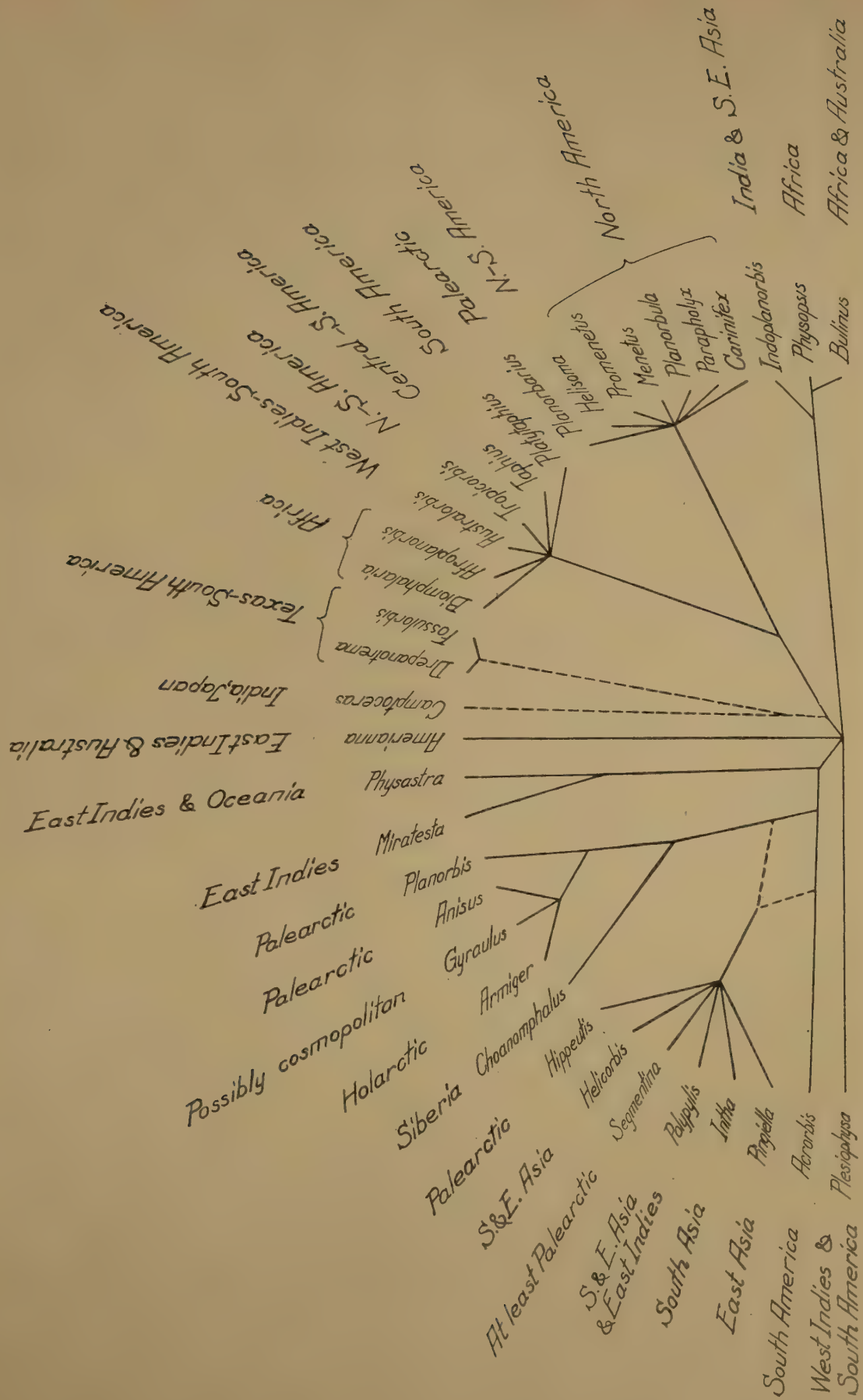
The African genera *Biomphalaria* and *Afroplanorbis* are undoubtedly congeneric. The genera *Australorbis* and *Tropicorbis*, which are mainly South American, do not differ in any essential way from the African forms. It is most likely that all of them can be placed in one genus, *Biomphalaria*. The South American genera *Taphius* and *Platytyphius* disagree in some comparatively superficial characters from one another and the above-mentioned genera. In another paper (Hubendick, 1955 a) it is shown that *Taphius* and *Platytyphius* are distinctly delimited neither from *Tropicorbis* nor from *Australorbis*. As there are no fundamental differences between the genera of the *Biomphalaria* tribe the most natural course should be to unite all the genera into one genus. Although this is justified from a purely zoological point of view, it is doubtful if it is wise to do so. The African and South American snail-hosts of *Schistosoma* belonging to the Planorbinae would then be called *Taphius*; this would certainly cause much confusion and trouble to workers in medical parasitology who are now familiar with names which are in current use. It seems wiser to keep *Biomphalaria* as a valid name for the African genera, *Australorbis* and *Tropicorbis*. All the snail-hosts of human Bilharziasis in those areas will then be included in the well-known genus *Biomphalaria*. *Taphius* and *Platytyphius* have either to remain as generically separated or to be included in *Biomphalaria*. The latter arrangement is to be recommended from a taxonomical point of view but requires certain nomenclatorial adjustments.

Drepanotrema and *Fossulorbis* are very closely related. Baker regards the latter as a subgenus of the former. *Fossulorbis* differs from *Drepanotrema* in having extremely reduced flagella. The distal genitalia show quite a wide range of variation within *Drepanotrema*. Further studies may show transitional forms between *Drepanotrema* and *Fossulorbis*. Until then it seems justified to keep the separate groups. There are similar relations between some groups belonging to the *Segmentina* tribe. *Anisus*, *Gyraulus* and *Armiger* are also very closely related. The anatomy of *Anisus sarasinorum* (Bollinger) shows, however, that we cannot define the definite limits of the genera until more species have been examined. In modern European literature *Gyraulus* and *Armiger* are generally united in one genus.

REMARKS ON DISTRIBUTION.

In reconstructing phylogeny on a comparative anatomical basis we are using only one cross-section of evolution, i.e. we are studying only the ends of the branches of the phylogenetical tree and only those ends which have survived to the present day. Conchological material alone is of no use for phylogenetic studies in the Planorbidae and therefore paleontological material is of little help. The present distribution of the planorbid groups should, at least theoretically, give some clues towards solving the phylogeny in the Planorbidae. However, the present distribution of the planorbid genera represent also a cross-section in their evolution, of which it is the result. In reconstructing this evolution, paleontological material can be of some help but it is too incomplete to allow any negative conclusions. It is of little importance, however, if the distributional conditions contradict the anatomical ones. If, on the other hand, the anatomical

Fig. 210.



Synoptic diagram showing the main distribution of the planorbis genera in relation to their taxonomic position.

and distributional facts correspond, the phylogenetical conclusions are slightly supported.

A synoptic diagram showing the relationships between probable taxonomical position and distribution of the conventional genera of Planorbidae is presented in fig. 210. There is, on the whole, fairly satisfactory agreement between taxonomical position and geographical distribution. The aberrant subfamily Plesiophysinae is restricted to the West Indies and some parts of South America. The physoid members of the subfamily Bulininae occur mainly in Africa and Australia. The occurrence of *Indoplanorbis* in India and South East Asia (including Sumatra) may represent a link though this genus is more evolved than the physoid forms.

The most primitive forms of the subfamily Planorbinae are present in the East Indies and the Pacific. The *Planorbis* tribe is Holarctic but *Gyraulus* is possibly cosmopolitan. *Anisus* also may prove to have a wider distribution. The *Segmentina* tribe is restricted to the Old World but ranges from Europe to the East Indies. *Acrorbis* is the only genus in South America with short marginal teeth. The *Biomphalaria* tribe is present on both sides of the Atlantic and it is known from Oligocene or Lower Miocene in both Africa and America. Lastly, the *Helisoma* tribe is, apart from the Palearctic *Planorbarius*, largely North American. *Planorbarius* is known from the Eocene; the other genera, except *Helisoma* which appeared during Miocene, did not appear until the Pliocene. Were it not for some extinct American groups which probably belong to the *Helisoma* tribe and are known from Eocene, it would be quite reasonable to assume that the tribe had its origin in the Palearctic region.

Secondary dispersals and incomplete paleontological knowledge make a reconstruction of the distributional evolution of the planorbid groups practically impossible. It seems, however, as most of the facts suggest, that the subfamily Planorbinae at least had its origin in the Palearctic region or in South or South-east Asia. The main conclusion here, however, is that the distribution of the planorbid genera support rather than contradict the phylogenetic results arrived at on a comparative morphological basis.

SUMMARY.

The taxonomic characters in the Planorbidae, their theoretical background and the general basis of their application have been discussed. The various characters have been critically reviewed. In practice the male copulatory organ and the radula have proved to be the most important structures for phylogenetic studies in the family. The prostate comes next in importance. Occasionally the pallial ridges, the jaw, the general shape of the shell, the central nervous system and the lateral appendages are important as characters for comparative studies. More rarely still other features are useful.

Representatives of almost all the planorbid genera have been examined morphologically and their phylogenetically important characters have been accounted for. The material examined includes the type species of twenty genera.

On a comparative morphological basis the family Planorbidae has to be divided up into three subfamilies, the Plesiophysinae, the Bulininae and the Planorbinae. The Plesiophysinae are aberrant and well separated from the other subfamilies.

The Bulininae are in the first place characterized by the presence of an ultra-penis. The evolution of the ultra-penis structure from the ordinary basommatophoran penis type is explained. Finally, the subfamily Planorbinae includes the greater majority of the planorbid genera.

The genera of the subfamily Planorbinae are shown to form nine groups. For various reasons the following characters can be regarded as more or less primitive in Planorbinae: a spired, sinistral shell, a moderately concentrated central nervous system, long marginal teeth with both posterior and lateral cusps, the presence of pallial ridges, a terminal pore on the penis, the absence of a flagellum or other appendages on the copulatory organ and a simple prostate. *Amerianna* on the one hand and *Physastra* with *Miratesta* on the other seem to be most closely related to the primitive planorbine form though they do not have all the primitive features. The remaining groups can be arranged in two main branches characterized by two different types of marginal teeth in the radula. The branch characterized by short marginals includes the genera which can be grouped under the *Planorbis* tribe and the *Segmentina* tribe as well as the genus *Acrorbis*. The branch characterized by long marginals includes the genera which can be grouped under the *Biomphalaria* and the *Helisoma* tribes. The genera *Camptoceras*, *Drepanotrema* and *Fossulorbis* may perhaps also belong to this branch.

In the *Segmentina* tribe and in the *Helisoma* tribe an accessory praeputial organ and an accessory duct between this organ and the upper end of the praeputial lumen or the penis sheath has evolved. These structures have almost certainly evolved independently in the two tribes. The probable origin of the structures has been reconstructed.

The most likely relationships within the family Planorbidae are presented diagrammatically in the figs. 181, 200 and 209.

The phylogenetically based classification present in this paper is critically compared with F. C. Baker's classification of the Planorbidae. Some remarks on the validity of various genera are also given.

A synopsis of the broad distribution of the conventional planorbid genera is given in fig. 210. It shows a fairly good correlation between relationship and distribution of the genera.

ACKNOWLEDGMENTS.

Several institutions, officials and private persons have enabled the present investigation to reach completion by procuring and sending spirit material of various planorbids to the author. He therefore wishes to take this opportunity to tender his gratitude to all involved. They are mentioned in connection with the accounts of the material examined under the respective genera. He also wishes to express his gratitude to Dr. W. J. Rees, British Museum (Natural History), who has revised the English in this paper.

ADDENDUM.

In a recent paper (The freshwater mollusks of Uganda and adjacent Territories. *Ann. Mus. Roy. Congo Belge (Zool.)*, 32:1, Tervuren 1954) Mandahl-Barth establishes the two new planorbid genera *Lentorbis* and *Segmentorbis*. Through the courtesy of Dr. Mandahl-Barth spirit material of one of the two species

referred to *Lentorbis* and of the genotype of *Segmentorbis* were made available for a completion of this investigation.

The shell of *Lentorbis* is similar to that of *Polypylis* but internal septa are usually lacking though they may be present as faint traces.

In *Lentorbis junodi* (Connolly) from Nawanga River in Eastern Uganda the mantle lobe is comparatively well developed. There is no pseudobranch and the anal pore is located posteriorly on the mantle lobe. Renal, dorsal and rectal ridges do not occur. According to Mandahl-Barth's description the radula is of the same type as in *Helicorbis* (cf. fig. 178 o). The male copulatory organ lacks flagella. The penis sheath is considerably longer than the praeputium. The penis is coiled within the penis sheath. There is no big lacuna in its tissue. The penis pore is terminal and there is no stylet. The fairly stout praeputium has two muscular pillars and the uppermost part of one of them is distinctly glandular. A big pendant structure branches off from the other pillar at about the middle of the praeputium. This structure is irregularly U-shaped in cross section, i.e., it forms a furrow. This is lined with an epithelium of comparatively big cells probably consisting of glandular cells alternating with slender ciliated cells. The prostate consists of several diverticula from a special prostate duct. The spermatheca is extraordinarily big.

The shell in *Segmentorbis* is variable but its general type is similar to that in *Segmentina* or *Polypylis*. Septa each consisting of three lamellae are present as in *Polypylis*.

The genotype of *Segmentorbis*, *S. angustus* (Jickeli) (material from Nawanga River, Eastern Uganda) has no mantle lobe and its pseudobranch is unfolded and simple. Renal, dorsal and rectal ridges do not occur. According to Mandahl-Barth the radula is of the same type as in *Lentorbis*. The male copulatory organ has probably only one flagellum. Histologically it belongs to the glandular type. No connection between the lumina of the flagellum and the penis sheath has been seen. The penis sheath is shorter than the praeputium and the penis is simple with a terminal pore. There are two muscular pillars in the comparatively slender praeputium, only one of them reaches the upper end of the structure. The prostate consists of a large number of diverticula from a special prostate duct. The spermatheca is fairly big and has an almost equally long, slender duct.

Both *Lentorbis* and *Segmentorbis* agree with the characters of the *Segmentina* tribe as far as the general shell type, the radula and the prostate are concerned. Their reproductive organs agree with those of *Segmentina* and *Hippeutis* in not having an accessory duct, and with *Hippeutis* in having a terminal penis pore without stylet or papilla. The organization of the muscular pillars in *Lentorbis* shows a slight resemblance to corresponding features in *Segmentina* but is rather aberrant in the tribe. The lack of flagellum is a definitely aberrant feature. The probable occurrence of only one flagellum (possibly without an efferent opening) in *Segmentorbis* also has to be considered as an aberrant feature.

The morphological conditions in *Lentorbis* and *Segmentorbis* support the impression that a more detailed classification within the *Segmentina* tribe, i.e., taxonomic evaluation of the genera and the solution of their mutual relationships, cannot be undertaken until much more material has been examined.

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KEY TO REFERENCE LETTERING TO TEXT-FIGURES.

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| <i>a.d.</i> , accessory duct. | <i>p.</i> , penis. |
| <i>a.g.c.</i> , accessory gland complex. | <i>p.a.p.o.</i> , projecting part of accessory praeputial organ. |
| <i>a.g.p.</i> , accessory gland pore. | <i>p.br.</i> , pseudobranch. |
| <i>a.p.</i> , anal pore. | <i>p.gl.</i> , praeputial gland. |
| <i>a.p.o.</i> , accessory praeputial organ. | <i>p.p.</i> , penis pore. |
| <i>c.c.</i> , complex cavity of the internal part of the accessory praeputial organ. | <i>p.p.gl.</i> , pore of praeputial gland. |
| <i>c.f.</i> , caudal end of foot. | <i>p.sh.</i> , penis sheath. |
| <i>c.m.</i> , circular muscles. | <i>pe.p.</i> , peripheral part of penis. |
| <i>c.p.</i> , central part of penis. | <i>pr.</i> , prostate. |
| <i>c.t.</i> , connective tissue. | <i>pr.d.</i> , prostate duct. |
| <i>cu.</i> , cuticula. | <i>prae.</i> , praeputium. |
| <i>d.r.</i> , dorsal ridge. | <i>prae.l.</i> , praeputial lumen. |
| <i>f.</i> , foot. | <i>rec.r.</i> , rectal ridge. |
| <i>fl.</i> , flagellum. | <i>ren.r.</i> , renal ridge. |
| <i>g.</i> , gill. | <i>s.</i> , slit in the accessory praeputial organ. |
| <i>g.p.</i> ♀, female genital pore. | <i>sec.</i> , secretion. |
| <i>g.p.</i> ♂, male genital pore. | <i>sp.</i> , spermatheca. |
| <i>gl.c.</i> , glandular cell. | <i>sp.d.</i> , spermathecal duct. |
| <i>i.a.p.o.</i> , internal part of accessory praeputial organ. | <i>spl.</i> , slit between ultra-penis and ultra-penis sheath or in the penis. |
| <i>l.m.</i> , longitudinal muscles. | <i>st.</i> , stiletto. |
| <i>m.</i> , muscle. | <i>t.</i> , tentacle. |
| <i>m.b.</i> , mantle border. | <i>u.</i> , uterus. |
| <i>m.c.</i> , mantle cavity. | <i>u.p.</i> , ultra-penis. |
| <i>m.fl.</i> , mantle flap. | <i>u.p.p.</i> , ultra-penis pore. |
| <i>m.l.</i> , mantle lobe. | <i>u.p.sh.</i> , ultra-penis sheath. |
| <i>m.o.</i> , mantle opening. | <i>v.d.</i> , vas deferens. |
| <i>m.p.</i> , muscular pillar. | <i>v.d.d.</i> , vas deferens distally to the prostate. |
| <i>m.t.</i> , muscular tissue. | <i>v.d.p.</i> , vas deferens proximally to the prostate. |
| <i>n.</i> , nerve. | <i>va.</i> , vagina. |
| <i>o.</i> , mouth. | <i>ve.</i> , velum. |

(Hatched areas indicate cut surfaces. Unless otherwise indicated the scale alongside each figure is 1 mm.)

The sexual skin of the Gelada Baboon (*Theropithecus gelada*)

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(With 3 plates)

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INTRODUCTION

Coloration and cyclic swelling of the sexual skin is well known in many species of monkey and ape. In the Gelada Baboon (*Theropithecus gelada* Rüpp.) the extent of the sexual skin and its intrinsic cyclic changes are particularly striking, and the latter are here described and illustrated for the first time. The nominal author has merely acted editorially to correlate Mr. Maurice Wilson's beautiful and accurate drawings with Head Keeper L. G. Smith's careful and extended observations, all based upon study of a group of these baboons lately living in the Society's Gardens at Regent's Park.

THE SEXUAL SKIN AND ITS CYCLIC CHANGES

The Gelada Baboon, a native of southern Abyssinia, shows marked sexual dimorphism. The male is a powerful animal and grows to a weight of about forty-five pounds, nearly twice that of the female, and is further distinguished by the presence of a mantle of long hair resembling a shoulder cape. Both sexes exhibit a triangular bare area of ventral throat skin with apex directed caudally and connected by a short, narrow, median groove with a second bare area, of inverted cordate shape, upon the front of the chest. These bare areas, the lower especially, are generally of a bright scarlet colour, the conspicuous red chest-patch accounting indeed for the Gelada Baboon's alternative vernacular name of "Bleeding-heart Baboon".

In the female the perineal sexual skin is a bare area extending dorsally from the pubes along the groins to the base of the tail, and expanded laterally into two conspicuous patches, one ventral to each ischial callosity, alongside the ventral vulva commissure. The cyclic changes occur not only in this perineal area of sexual skin but also in the bare triangular and cordate cutaneous areas

of the neck and chest. The changes involve a waxing and waning in intensity of the red coloration and a tumescence of the areas, but the most striking change is the development of numerous, more or less symmetrical, pearly cutaneous vesicles at the margins of these pigmented areas.

When the female reaches puberty at about five years of age the bare areas attain their maximal pigmentation, and the vesiculation becomes manifest by the development of a few pearl-like blisters at the lower edges of the neck patch. These vesicles gradually increase in number and extend on to the chest until all the bare areas are circumscribed thereby. The rows of vesicles defining the outline of the triangular neck patch (one along its base, the others along its two sides) give the appearance of two pearl necklaces. Where these rows meet at the lateral extremities of its base there is a larger, wart-like protuberance which does not undergo cyclic change. The vesicles circumscribing the cordate breast-patch are larger and pear-shaped; they hang by their smaller ends with their larger ends free. (At puberty the teats, which during immaturity have remained small and widely spaced, become enlarged, pear-shaped, and bright red, and now depend in close proximity on each side of the mid-line.) When the vesicles surrounding the bare area of the chest make their appearance, vesicles also appear in association with the perineal area of sexual skin: one row of such is developed along the ventral margin of each ischial area, another group appears simultaneously on the pubis and yet another on each side of the base of the tail. Thus the perineal sexual skin is circumscribed by vesicles in precisely similar fashion to the thoracic bare area.

As menstruation approaches, the sexual skin loses its intense colour and, fading to a delicate flesh pink, becomes pallid and taut: simultaneously, the vesicles become enlarged and fluid-filled. The tumid condition persists for several days. Thereafter the vesicles gradually diminish in fullness and the skin regains its vivid scarlet colour, together with its customary more flaccid condition. Menstruation occurs within a few days of vesicular recession: it lasts for two or three days and the discharge is slight compared with that in other species of baboon. Vesiculation does not invariably disappear completely before the onset of menstruation. A few days after the cessation of the discharge vesiculation reappears. The complete cycle occupies from thirty-two to thirty-six days.

The female Gelada Baboon manifests generally a notably timid disposition which during menstruation becomes intensified, even towards the male. Her confidence returns, however, with the redevelopment of the vesicles; when these have attained their maximal development she spends much time contentedly grooming the male, and is equally aggressive should danger threaten. During grooming the animals converse in subdued, plaintive tones, and coition takes place after lengthy periods of such social intercourse.

No experimental work is available concerning correlation of the sexual skin cycle with the phases of ovarian activity. It may be suggested, however, that the development of the vesicles and the intensified coloration of the skin are controlled by the follicular phase of the ovarian cycle, and the pallor of the skin, together with the intense vesicular tumescence, by the luteal phase. As the luteal

phase passes the vesicles diminish, to redevelop, together with an intensified coloration of the bare areas, at the onset of the subsequent follicular phase.

SUMMARY

In the Gelada Baboon there are two areas of bare pigmented sexual skin, one on the chest, the other in the perineal region. Cyclic swelling and intensification of the red colour of this sexual skin is accompanied by the associated development of conspicuous, circumambient, cutaneous vesicles.

PLATE 1

PLATE 1

Female Gelada Baboon

- Fig. 1. Intermenstrual phase, the skin brightly coloured, and the vesicles moderately distended.
- Fig. 2. Immediate pre-menstrual phase. The skin pale and the vesicles greatly distended.

(Both figures are from drawings by Maurice Wilson.)



1



2

Sexual skin of the female Gelada Baboon.

PLATE 2

PLATE 2

Female Gelada Baboon

- Fig. 3. Pre-menstrual phase with large vesicles on the ischial and subcaudal regions.
- Fig. 4. Post-menstrual phase; the coloration returning to the skin and the vesicles beginning to regain their tumidity.

(Both figures are from drawings by Maurice Wilson.)



3



4

Sexual skin of the female Gelada Baboon.

PLATE 3

PLATE 3

Photograph of a female Gelada Baboon in the inter-menstrual phase. The two "necklaces" are seen meeting at the caruncles at each side of the neck which do not undergo cyclic swelling. The vesicles on the chest are conspicuous. The two large swellings at the base of the cleft between the breasts in the mid-line are the teats. (Photo: R. C. N. Neale.)

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